# A revision of the Morinaceae (Magnoliophyta Dipsacales) 

Margaret J. Cannon and John F. M. Cannon<br>Department of Botany, British Museum (Natural History), Cromwell Road, London SW7 5BD

## Contents

Synopsis ..... 1
Introduction ..... 2
Historical summary ..... 2
Relationships of Morina sensu lato (Morinaceae) within the Dipsacales ..... 3

1. Morphology ..... 3
2. Embryology ..... 4
3. Cytology ..... 4
4. Palynology [by S. Blackmore] ..... 5
5. Conclusions ..... 7
Genera of the Morinaceae ..... 7
Systematic treatment ..... 8
Morinaceae ..... 8
Key to the genera ..... 9
I. Acanthocalyx (DC.) M. Cannon ..... 9
Key to the species ..... 11
6. A. nepalensis (D.Don) M. Cannon ..... 12
7. A. delavayi (Franchet) M. Cannon ..... 12
8. A. alba (Hand.-Mazz.) M. Cannon ..... 14
II. Cryptothladia (Bunge) M. Cannon ..... 15
Key to the species ..... 17
9. C. chinensis (Pai) M. Cannon ..... 17
10. C. parviflora (Karelin \& Kir.) M. Cannon. ..... 18
11. C. kokonorica (Hao) M. Cannon ..... 19
12. C. chlorantha (Diels) M. Cannon ..... 19
13. C. polyphylla (Wallich ex DC.) M. Cannon. ..... 20
14. C. ludlowii M. Cannon ..... 22
III. Morina L ..... 24
Key to the species ..... 24
15. M. kokanica Regel ..... 26
16. M. coulteriana Royle ..... 26
17. M. persica L. ..... 28
18. M. longifolia Wallich ex DC. ..... 30
Specimens examined ..... 31
Acknowledgements ..... 34
References ..... 34
Taxonomic index ..... 35

## Synopsis

The group of species comprising the genus Morina is reviewed, and support is established from the fields of comparative morphology, embryology, cytology, and palynology, to justify their recognition as a distinct family, Morinaceae J. Agardh, related to the Dipsacaceae. Three clearly defined groups are recognised
within Morina sensu lato and, as a consequence, the sections Acanthocalyx DC. and Cryptothladia Bunge are elevated to generic status. Three new combinations under Acanthocalyx and five under Cryptothladia are made, and a new species $C$. ludlowii is described. Thirteen species are recognised as occurring in the family.

## Introduction

This study was begun by one of us (J.F.M.C.) and, after a lapse of some years, was resumed by both authors. Much of the detailed examination of specimens, measurement of organs, and description of taxa was done by one author (M.J.C.), but the conclusions and consequent taxonomy are the result of close collaboration and joint decision. So that future botanical literature will not be unnecessarily burdened by dual author citations, we have decided that only one of us (M.J.C.) will appear as the author of the new taxa and combinations. Unless otherwise stated, all the specimens cited have been seen by the authors.

The Morinaceae includes a range of species that present fascinating problems in relationships both within and outside the group. It is hoped that this revision will not only stimulate further research, but will also encourage discerning plantsmen to grow a range of species beyond the relatively well-known and quite widely cultivated Morina longifolia.

## Historical summary

The genus Morina was first described by Tournefort in 1703, in honour of Ludovic Morin, a doctor of medicine of Paris and a member of the Academy of Sciences of that city. It was subsequently renamed Diototheca - a reference to the ear-like lobes of the calyx - by Vaillant in 1724 (subsequently misspelt by later authors Diolotheca, Diodotheca, and Dictotheca), and placed by him in his class Dipsacées, between Pterocephalus and Valeriana. In both cases the concepts were based on Morina orientalis carlinae folio, the only species known at the time and now known as Morina persica L .

The genus passed into the era of binomial nomenclature in the first edition of Species Plantarum (1753), when Linnaeus based his concept on his treatment in Hortus Cliffortianus (1738), and beyond that on Tournefort's (1703) original publication. In 1820, Rafinesque separated Morina and Diototheca (misspelt by him as Diolotheca) from the Dipsacaceae as the new family Morinidia, and considered this to be more nearly related to the Valerianaceae. Coulter in 1824 included Morina in the Dipsacaceae, although he recognised many differences, and de Candolle in 1830 continued to regard it as a member of that family, a view that was followed by Bentham \& Hooker in 1873.

Spach in 1841 classified Morina in the Dipsacaceae, but in a footnote says it has many affinities with the Valerianaceae, and ought to be regarded as a monogeneric family between the Valerianaceae and the Dipsacaceae. Bunge (1852) divided the genus into three sections: Cryptothladia Bunge - M. parviflora only; Diotocalyx DC. - comprising M. persica, M. elegans, M. longifolia, M. polyphylla, M. lehmanniana, and M. coulteriana; and Acanthocalyx DC. consisting of M. nana only. Van Tieghem (1909) recognised the Morinaceae J. Agardh as a separate family, and distinguished it from Dipsacaceae by a number of morphological characters, pointing out that this left the Dipsacaceae as a much more homogenous family.

In 1938, Pai reviewed the Chinese species of Morina, recognising six species in two sections (Acanthocalyx and Diotocalyx). He discussed the relationships of the additional species that had been found as a result of the exploration of western China, notably by Forrest, Handel-Mazzetti, and the French missionary collectors.

Embryological and cytological studies by Pouques in 1949, Vijayaraghavan \& Sarveshwari in 1968, and Kamelina in 1976 and 1977 provide strong evidence for the retention of the Morinaceae as a separate family, as do recent palynological studies by Blackmore \& Cannon (1983). In her thesis Verlaque (1976) separated the Morinaceae from the Dipsacaceae on cytological grounds, and considered its origins to lie within the Valerianaceae, while in her later publication (Verlaque 1977), she tabulates the differences between all three families in morphology, cytology, and phytogeography.

Authors of major reviews of the flowering plants during the last 20 years have remained divided as to whether or not to recognise the Morinaceae. Wagenitz (1964), Hutchinson (1973), Heywood (1978), and Cronquist (1981) all include Morina in the Dipsacaceae, but agree that many anomalous characters are involved. Thorne (1976) prefers to retain the Morinaceae, and Takhtajan (1954) notes that it is a distinct family and refers to the work of Vijayaraghavan \& Sarveshwari (1968) and Kamelina \& Yakovlev (1974), stating that the work of the last authors demonstrates that it is near the Caprifoliaceae.

## Relationships of Morina sensu lato (Morinaceae) within the Dipsacales

## 1. Morphology

It is generally agreed that Morina sensu lato must be placed in the Dipsacales, probably in the Dipsacaceae, or in the Valerianaceae, or between them. There are, however, many difficulties in placing it in either family, or even in regarding it as an intermediate. Many authors have placed Morina in the Dipsacaceae, the most outstanding similarity being the possession by both of involucels. Van Tieghem (1909) and others have pointed out that this character is not confined to the Dipsacaceae, and occurs also in some genera of the Valerianaceae, some Compositae, as well as in the Nyctaginaceae. Morphologically, Morina sensu lato is set apart from the Dipsacaceae by the possession of a verticillate inflorescence, whorled leaves (not in Acanthocalyx), the nature and form of the involucel and calyx, the aestivation of the corolla, the insertion of the stamens (and staminodes) in 2 ranks, the ovary with 3 united carpels with 2 obsolete, and the 6 -veined achene. It resembles the Valerianaceae in the number of carpels, the zygomorphic corolla, and in some cytological characters (see account of cytology). The Valerianaceae and Dipsacaceae are usually separated by the reduction or sometimes lack of a conspicuous involucel in the Valerianaceae, the type of inflorescence, and the tricarpellate or bicarpellate ovary. Table 1 summarises the differences between the two families and Morina sensu lato.

Table 1 Summary of morphological differences between Morina sensu lato and the Dipsacaceae and Valerianaceae.

| Morina sensu lato | Dipsacaceae | Valerianaceae |
| :---: | :---: | :---: |
| Leaves often whorled (not Acanthocalyx) | Leaves opposite | Leaves opposite (sometimes all basal) |
| Inflorescence verticillate | Inflorescence capitulate | Inflorescence cymose |
| Involucel 12-nerved (formed from fusion of 4 bracteoles) | Involucel 8-nerved (formed from fusion of 2 bracteoles) | Involucel usually absent (8-nerved in Triplostegia) |
| Calyx zygomorphic (2-lobed or sheathing) | Calyx actinomorphic or obsolete | Calyx actinomorphic or obsolete |
| Corolla lobes in bud with posterior lobes overlapping the 2 lateral lobes of anterior lip | Corolla lobes of bud with 2 lateral lobes of anterior lip overlapping the posterior lobes |  |
| Stamens 2 (with 2 staminodes) or 4 of 2 differing lengths | Stamens 4 - all equal | Stamens $1,2,3$ or 4 equal |
| Ovary of 3 united carpels -2 obsolete | Ovary of 2 united carpels <br> -1 obsolete | Ovary of 3 united carpels - 2 reduced and empty or obsolete |
| Achene 6-veined | Achene 8-veined | Achene 8-veined |
| Nectaries at base of filaments | Nectaries round base of style | Nectaries often in spur or sac at base of corolla |

## 2. Embryology

The relationships of Morina sensu lato with the Dipsacaceae was extensively studied by Vijayaraghavan \& Sarveshwari (1968). They concluded that M. longifolia resembles the Dipsacaceae in only a few embryological features, such as the dicotyledonous type of anther wall development, the anatropous ovule, a Polygonum type of embryo sac, and the cellular endosperm. It differs in many other characters, such as a persistent middle layer in the anther, secretory anther tapetum, pollen grains shed at the 2-celled stage, absence of integumentary vascular bundles, persistent pollen tube, ephemeral uninucleate antipodal cells, ruminate endosperm, transverse division of the zygote, and Solenad type of embryogeny. They considered that there were so many major differences that Morina could not be considered as a genus of the Dipsacaceae. They made no reference to possible relationships with other groups of the Dipsacales. However, Crété (1963) stated that both Dipsacaceae and Valerianaceae could be referred to the Seneciad type of embryogeny, which is far removed from the Solenad in his classification. Table 2 summarises the embryological differences between Morina longifolia and the Dipsacaceae.

Table 2 Summary of embryological and related characters (after Vijayaraghavan \& Sarveshwari 1968).

| Feature | Morina longifolia | Dipsacaceae |
| :--- | :--- | :--- |
| Anther wall | Dicotyledonous type | Dicotyledonous type |
| Endothecium | Fibrous | Fibrous |
| Middle layer | Persistent | Ephemeral |
| Tapetum | Secretory | Periplasmodial |
| Microspore tetrad | Tetrahedral or isobilateral | Tetrahedral |
| Shedding stage of pollen | 2-celled | 3-celled |
| Staminodes | Present | Absent |
| Ovule | Anatropous, unitegmic and | Anatropous, unitegmic |
|  | tenuinucellar | and tenuinucellar |
| Integumentary vascular | Absent | Present |
| bundles |  |  |
| Hypostase | Present but no cavities | Present, cavities contain |
|  |  | Pollow liquid |
| Embryo sac | 3-nucleate type | Polygonum type |
| Antipodal cell | Cellular, ruminate | 3, uni or binucleate |
| Endosperm | Persistent | Cellular, non-ruminate |
| Pollen tube | Divides by transverse wall | Not persistent |
| Zygote | Solenad type | Pivides by vertical wall |
| Embryogeny | Only outer epidermis persists | Not known |
| Testa | as a flimsy layer |  |

## 3. Cytology

The following chromosome counts have been recorded for Morina sensu lato:

| $\left.\begin{array}{ll}\text { Morina persica } \mathrm{L} . & 2 \mathrm{n}=34 \\ \text { Morina longifolia Wallich ex DC. } & 2 \mathrm{n}=34\end{array}\right\} \quad$Kachidze (1929) and <br> Verlaque (1976 \& 1977) <br> Morina kokanica Regel | $2 \mathrm{n}=34$ |
| :--- | :--- |$\quad$| Verlaque (1976 \& 1977) |
| :--- |

In the Dipsacaceae, base numbers of $x=5,7,8,9$, and 10 are known with various polyploids, but $2 \mathrm{n}=34$ appears nowhere in the lists. A similar situation is recorded for the Valerianaceae, with base numbers of $x=7,8,9$, and 11. The early count noted by Risse (1929) for Morina longifolia
as $2 n=16$ has not been substantiated, and must be regarded as dubious in the absence of further support. Poucques (1949) considered Morina to differ from the Dipsacaceae in the homogenous, euchromocentric nucleus, and in the number and form of the chromosomes, remarking on their very small size. He recorded the resting nucleus to be $6-7 \mu$, with one nucleolus. Verlaque (1976 \& 1977) studied three species of Morina and confirmed the findings of Poucques (1949). She found the chromosomes at metaphase to be $0.7-1 \cdot 5 \mu$, differing markedly in size from the Dipsacaceae $(1-5 \mu)$ and the Valerianaceae $(0 \cdot 7-4 \mu)$. The centromere was scarcely visible (more or less visible in the Valerianaceae and strongly marked in the Dipsacaceae). The resting nucleus was homogenous and euchromocentric in both Morina and the Valerianaceae, but granulo-reticulate in the Dipsacaceae. She concluded that the origin of Morina should be looked for in the Valerianaceae. Cronquist (1981) referred to fibrous thickenings being present in all layers of the anther and connective in Morina, but only in the endothecium and sometimes the endodermis in the Dipsacaceae, and the sperms of Morina as having a little cytoplasm, whilst those of the Dipsacaceae are naked.

## 4. Palynology*

## by S. Blackmore

Morinaceae pollen, which has been studied by Erdtman (1945, 1960a), Vinokurova (1959), and Blackmore \& Cannon (1983), is morphologically distinctive and diverse. Three main pollen types, based on light microscopy of acetolysed (Erdtman, 1960b) pollen, are distinguished here (Fig. 1).
1a. Pollen without prominent equatorial protrusions, ectoapertures colpate. Acanthocalyx-type
1b. Pollen with three prominent equatorial protrusions, ectoapertures porate:
2a. Equatorial protrusions domed, internal outline of pollen hour-glass shaped. Cryptothladia type
2b. Equatorial protrusions funnel shaped, internal outline of pollen similar to external. Morina type

## Acanthocalyx type

Pollen tricolporate; triangular in polar view with the colpi in the rounded angles, subrhomboidal in equatorial view. Ectoapertures broad colpi one third as long as polar axis, endoapertures transverse colpi fused into a continuous equatorial band (zonorate). Exine thick, $6 \mu \mathrm{~m}$ at poles increasing to $10 \mu \mathrm{~m}$ at colpus margins; sexine spongy, without distinct columellae; tectum smooth with sparse microperforations. Polar axis $120-150 \mu \mathrm{~m}$ long, equatorial axis $100-125 \mu \mathrm{~m}$.

Occurs in all species of Acanthocalyx.

## Cryptothladia type

Pollen tripororate; rounded to triangular in polar view, prolate in equatorial view with prominent domed equatorial protrusions. Ectoapertures pores situated in the equatorial protrusions, endoapertures transverse colpi fused to form a narrow equatorial band (zonorate) flanked by very marked thickening of the nexine. Exine thick, $5 \mu \mathrm{~m}$ at the poles, $12 \mu \mathrm{~m}$ at the apertures; sexine spongy, thinner than nexine except at poles. Tectum smooth with scattered microperforations towards the equator. Polar axis $100-120 \mu \mathrm{~m}$ long, equatorial axis $55-70 \mu \mathrm{~m}$ (including protrusions).

Occurs in all species of Cryptothladia with some variation in the thickening of the sexinous walls of the protrusions and the size of pores.

## Morina type

Pollen tripororate; rounded to triangular in polar view, prolate to nearly cylindrical in equatorial view with large funnel shaped equatorial protrusions prominent in either orientation. Ectoapertures pores at the mouth of each funnel shaped protrusion, endoapertures pores, sometimes with a very slight thinning of the inner nexine surface between them. Exine thick, $6 \mu \mathrm{~m}$ at poles increasing to $12 \mu \mathrm{~m}$ at equator; sexine and nexine equal at poles, nexine much thicker at equator. Tectum smooth at poles but often with two parallel bands of verrucae between each


Fig. 1 Scanning electron micrographs of pollen types. Scale lines $20 \mu \mathrm{~m}$.

1. Acanthocalyx-type, A. nepalensis (Polunin, Sykes \& Williams 4536 ), slightly oblique equatorial view showing a colpate ectoaperture.
2. Morina-type, M. persica (Davis, Dodds \& Cetik 19068), slightly oblique polar view showing verrucate ornamentation at equator.
3. Cryptothladia-type, C. chinensis (Licent 4548 ), equatorial view showing domed apertural protrusions.
4. Morina-type, M. coulteriana (Vassiljeva 5487), equatorial view showing funnel shaped apertural protrusions.
protrusion, microperforations more numerous towards the equator. Polar axis $150-270 \mu \mathrm{~m}$ long, equatorial axis $120-160 \mu \mathrm{~m}$ (including protrusions).

Occurs in all species of Morina sensu stricto with some variation in ornamentation, size, and shape.

## Discussion

Pollen grains of Morinaceae differ from those of the Dipsacaceae in having spongy rather than columellate sexine, lacking operculae over the apertures, and in their unusual pre-germinative processes (Blackmore \& Cannon, 1983). The zonorate endoapertures of two of the Morinaceae pollen types have no counterpart in the Dipsacaceae and are probably secondarily absent from the third pollen type. Similarly the domed and funnel shaped protrusions of Cryptothladia and Morina sensu stricto are unlike any apertural structures in the Dipsacaceae.

## 5. Conclusions

Major differences in morphology, palynology, embryology, and cytology have been shown to occur between Morina sensu lato (now regarded by us as three quite distinct genera, Morina, Cryptothladia, and Acanthocalyx), and the other members of the Dipsacales. The verticillate flower arrangement, the nature and form of the calyx, the androecium, and the zygomorphic ovary and achene are perhaps the most significant morphological features in this respect. The pollen is most unusual, showing few similarities with any other, either within the Dipsacales or with that of any other order of flowering plants. By palynological standards, these features alone strongly suggest recognition at the family level. Embryological and cytological studies have been made, so far as is known, only on members of the genus Morina sensu stricto, but it seems probable that Cryptothladia would resemble Morina in these characters, while the position of the less-closely related Acanthocalyx is not clear. Further wide-ranging research on these to genera would be most welcome. The weight of evidence from these four fields is very much in favour of the recognition of the Morinaceae as a distinct family within the Dipsacales.

## Genera of the Morinaceae

The genus Morina has often been separated into two or three taxa (de Candolle (1830), Bunge (1852), van Tieghem (1909)) solely on grounds of morphology. Our studies on the comparative morphology of the group, and especially of its remarkable palynology, have convinced us that the Morinaceae is best considered to comprise three quite distinct genera.

Acanthocalyx differs from the other two genera in so many ways, that differences are easier to list than similarities. The most striking features are leaf arrangement, calyx shape, corolla shape, stamen number, and achene shape. Table 3 summarises these distinctions.

Table 3 Characters distinguishing Acanthocalyx from Cryptothladia and Morina sensu stricto.

| Acanthocalyx | Cryptothladia and Morina sensu stricto |
| :--- | :--- |
| Leaves opposite | Leaves whorled |
| Flowers in close verticels to <br> subcapitate | Flowers in well-separated verticels or in <br> ( cylindrical spikes of verticels |
| Calyx mouth obliquely cut, often <br> with 2 lateral and 3 (rarely 1) <br> posterior teeth, not laminate | Calyx distinctly 2-lobed, laminate |
| Corolla $\pm$ 2-lipped, lobes often | Corolla markedly zygomorphic, 2-lipped, |
| nearly equal | lobes unequal <br> Stamens 4 |
| Stamens 2, with 2 sterile stamens or minute <br> staminodes |  |
| Nectary dome shaped, regular | Nectary with 3 lobes or with 2 irregularly <br> lobed nectaries |

Diotocalyx, the section recognised by de Candolle in contrast to his section Acanthocalyx, is here divided between the genera Morina sensu stricto and Cryptothladia. These genera are separated by the size and shape of the corolla, the shape and position of the staminodes or sterile stamens, the number and shape of the nectaries, and the pollen characters already described in detail. Table 4 summarises the major morphological differences.

Table 4 Morphological characters distinguishing Morina sensu stricto and Cryptothladia. See Fig. 2.

## Cryptothladia <br> Morina sensu stricto

Corolla equalling or shorter than the calyx
Corolla 2-4 lobed (sometimes scarcely 5 -lobed), limb scarcely expanded, posterior lip entire, slightly toothed or barely 2-lobed
Sterile stamens 2 , lobes equalling or exceeding those of the fertile stamens, at the base of the corolla tube or a short way above Flowers probably cleistogamous

Corolla much exceeding the calyx
Corolla clearly 5-lobed, limb expanded, posterior lip markedly 2-lobed, anterior lip markedly 3-lobed

Staminodes 2, minute, much smaller than the fertile stamens, attached in the corolla throat just below the fertile stamens
Flowers not obviously cleistogamous


B


Fig. 2 Diagram showing relative positions of fertile stamens, sterile stamens, and staminodes in (A) Acanthocalyx, (B) Cryptothladia, and (C) Morina.

## Systematic treatment

Morinaceae J. Agardh, Theoria systematis plantarum: 234 (1858).
Morinidia Raf. in Annls gén. Sci. phys. Brusc. 6: 88 (1820).
Type genus: Morina L.
Perennial herbs with rootstocks often covered with the remains of old leafbases. Leaves opposite or whorled, exstipulate, often spiny, the petioles often connate, forming loose
cylindrical sheaths. Flowers hermaphrodite, zygomorphic, in verticillasters or subcapitulate heads of biparous cymes. Involucel (epicalyx) of 4 fused bracteoles, smooth, with few numerous spiny teeth or setae, 12 nerved. Calyx epigynous, cupular, with an obliquely cut mouth, or 2-lobed. Corolla tubular, scarcely to markedly 2 -lipped, lobes 5 , spreading, or $2-5$ scarcely opening, the 2 lateral lobes of the anterior lip overlapping the median and the 2 posterior lobes overlapping them in bud. Stamens 4 , all fertile, borne near the corolla mouth, one pair above the other; or with 2 fertile borne near the corolla mouth or halfway up the tube, and 2 sterile stamens (staminodes) borne at the base of the corolla or halfway up the tube. Anthers introrse, 2-celled, the lobes subequal or markedly unequal, opening longitudinally. Ovary inferior, 1 -locular, formed by the fusion of 3 carpels, 6 -veined, adherent to the calyx tube; ovule solitary, pendulous, style slender, stigma simple. Fruit dry, indehiscent, enclosed in the involucel and surmounted by the persistent calyx.

Morinaceae differs from Dipsacaceae in its often whorled leaves, the flowers in cymose verticillasters (sometimes subcapitulate, but almost always with at least one detached lower verticell), the venation and form of the involucel, aestivation, and the 6 -veined ovary. It also differs in many detailed palynological and embryological features and in chromosome numbers. These are detailed in the appropriate introductory sections.

## Key to the genera

1a. Stamens 4; calyx limb oblique; plants not thistle-like
I. Acanthocalyx (p. 9)
1b. Stamens 2 plus 2 staminodes; calyx limb 2-lipped; plants thistle-like:
2a. Corolla up to 1 cm , almost hidden by the much longer calyx, weakly lobed with 2 or 4 major lobes; staminodes at base of corolla tube ( $1 / 3$ way up the tube in C. chinensis)
II. Cryptothladia (p. 15)

2b. Corolla $2-5 \mathrm{~cm}$ long, well exserted from the calyx, strongly 5 -lobed; staminodes borne $1 / 2$ way up corolla tube
III. Morina (p. 24)

See Figs 4, 6, and 9 .

## I. ACANTHOCALYX (DC.) M. Cannon, stat. nov.

Morina Section Acanthocalyx DC., Prod. 4: 644 (1830).
Type species: Acanthocalyx nepalensis (D.Don) M. Cannon
Plants perennial, with a woody rootstock, often covered with the remains of old leaf bases. Leaves opposite and decussate, linear, lanceolate or ovate, with or without spines or short setae. Petioles joined to form a sheath, usually with 2 lines of hairs continued down the internode. Uppermost leaves often more spiny at the base. Inflorescence subcapitulate, often with one or more whorls of flowers below the primary head. Bracts free, connate or sheathing at the base. Flowers sessile, shorter than the bracts, at least at the base. Involucel campanulate, very fragile and papery at anthesis, enlarging and becoming more coriaceous in fruit, persistent, with few to numerous teeth. Calyx cylindrical, the mouth obliquely cut, with a ventral fissure, often with 2 lateral and 3 posterior subspinose teeth, the laterals sometimes overlapping the fissure and becoming sheathing. Corolla cylindrical, somewhat swollen below the limb with two posterior and 3 anterior spreading lobes. Stamens $4, \pm$ equal, inserted just below the swollen part of the corolla tube, scarcely emergent from it, anthers introrse, sub-equal. Nectary small, spherical at the base of the corolla tube. Style equalling or exceeding corolla tube, stigma disc-shaped. Ovary unilocular, ovule pendulous. Achenes smooth or rugose, apex somewhat cup-shaped.

Three species of Acanthocalyx are recognised by us: A. nepalensis, widely distributed in Nepal, but spreading into Bhutan, Yunnan, Sichuan, and Xizang, A. alba (including Morina leucoblephara Hand.-Mazz.), occurring mainly in western China and Xizang, and A. delavayi, distributed mainly in Yunnan, Sichuan, and Gansu. See Fig. 3.

Fig. 3 Distribution of Acanthocalyx species: A. nepalensis $(\bullet)$, A. delavayi $(\mathbf{\Delta})$, A. alba $(\boldsymbol{\bullet})$, and
intermediates $(\triangle)$.

## Key to the species

1a. Corolla pink or purplish, straight or slightly curved:
2a. Corolla tube hairy beneath, often somewhat curved, ovary glabrous ........... 1. A. nepalensis (p.12)
2b. Corolla tube nearly glabrous beneath, straight, ovary pubescent ...................2. A. delavayi (p. 12)
1b. Corolla white or cream, markedly curved ...................................................... 3. A. alba (p. 14)
The species of Acanthocalyx are difficult to distinguish and Table 5 of diagnostic characters is provided to supplement the key.

Table 5 The species of Acanthocalyx compared.

|  | alba | nepalensis | delavayi |
| :--- | :--- | :--- | :--- |
|  | $(5-) 6-7(-12)$ | $(9-) 11-12 \cdot 5(-14)$ | $(7-) 10-14(-15)$ |
| Calyx length $(\mathrm{mm})$ | $1-2 \cdot 5$ | $1-6 \cdot 5$ | $0 \cdot 5-5 \cdot 5(-9)$ |
| Calyx tube length $(\mathrm{mm})$ | + | $+(-)$ | 0 |
| Corolla curve | few | + | few to + |
| Corolla hairs below | + | + | pink |
| Corolla hairs above | white (or cream) | pink | $(2-) 2 \cdot 5-4$ |
| Corolla colour | $1 \cdot 1-1 \cdot 7$ | $(1 \cdot 4-) 1 \cdot 8-2 \cdot 1$ | $6 \cdot 25-9(-10)$ |
| Width of corolla tube (mm) | $11 \cdot 8-20$ | $9-11$ | $(0-)$ top $0 \cdot 5-$ |
| Ratio width/length | $0-$ very few | on top $0 \cdot 5-1 \cdot 5 \mathrm{~mm}$ | $2 \mathrm{~mm}(-$ base $)$ |
| Hairs inside involucel | on veins) |  |  |
| (14-) $16(-17)$ | $9-15(-16)$ | $20-22(-30)$ |  |
| Involucel teeth | + | 0 | + |
| Ovary hairs | lanceolate (rarely | linear to narrowly | (broadly) ovate |
| Leaf shape | linear lanceolate) | lanceolate | -lanceolate to |
|  |  |  | lanceolate |

A number of specimens are difficult to allocate to the three species recognised. By far the largest number of these are found in gatherings from Yunnan and Sichuan, e.g. McLaren's collectors 309D, B73, Potanin on 29.6.1983, Pratt 45, Rock 17725, and most collections of this genus made by Maire. These gatherings appear to correspond with A. delavayi, except for the ovaries which are glabrous. A few are similar in most respects to $A$. nepalensis, but have pubescent ovaries (e.g. Forrest 7155) or two lines of hairs on the ovary (Ludlow, Sherriff \& Hicks 16573). A few gatherings from Yunnan and Sichuan include plants with both pink and white flowers, e.g. Pratt 232; these are probably colour variants within the circumscription of $A$. alba. Certain collections from Xizang, e.g. Soulie 71 and Dr King's collector 8, probably have specimens of $A$. alba and $A$. delavayi mixed on the same sheet. A gathering from Xizang (Morton? 232) resembles $A$. nepalensis in most respects, but is recorded as having white flowers. This may be an albino form of A. nepalensis or may involve a label error. The large number of gatherings of intermediates and mixed collections suggest that different species often occur in close proximity. This could imply that hybrids are frequent, and/or that the group is still incompletely differentiated and that speciation is still continuing. However, until the situation can be properly analysea using a range of experimental techniques on living plants, especially from areas where ranges overlap, we prefer to draw attention to the variation by recognising three species within Acanthocalyx, rather than to obscure the evidence by taking the easier option of recognising one taxon only at the species level.

Pai (1938) recognised four species, but this approach does not seem to be supported by our own observations. In his key characters used are the ciliate-spinose or densely ciliate nature of the lower leaves, but this seems to us to be completely variable in all species; the corolla lobes are said to be unequally lobed in Morina betonicoides (= Acanthocalyx nepalensis) and equally lobed in Morina alba. Both species seem to us to have more or less unequally lobed corollas, the upper two lobes being somewhat smaller than the lower three, and the two lateral lobes of the lower lip being rather narrower than the central lobe. $M$. betonicoides is said to have emarginate
corolla lobes, whilst $M$. alba has undulate-crenulate lobes, but this does not seem to be the case in the many specimens we have examined.

## 1. Acanthocalyx nepalensis (D. Don) M. Cannon, comb. nov.

Fig. 4.
Morina nepalensis D. Don, Prod. Fl.Nepal.: 161 (1825). Type: In Gossainthan Nepalensium, Wallich [presumed to be Wallich 424 (BM; E; K - type collection).
Morina nana Wallich ex DC., Prod. 4: 645 (1830). Type: Gossain Than, 1824, Wallich 424 (BM; E; K type collection).
Morina betonicoides Benth., in Ic. Pl. 12, t. 1171 (1873). Type: Sikkim, 3400-3600 m, 12.7.1849, Hooker s.n. (K - holotype; BM - isotype).

Low perennial herbs, with short woody rhizome, covered with remains of old leaf bases. Leaves of sterile shoots entire, narrowly lanceolate or linear, glabrous or green above, glabrous and paler beneath, with midrib and 2-4 nearly parallel raised veins, with subspinose setae (rarely absent) on the margin, up to 20 cm . Fertile shoots erect, up to 35 cm (rarely to 50 cm ), with leaves similar to those of the sterile shoots, except for the lowest pair, which are often small, nearly ovate or spathulate, membranous and spineless. Upper stem leaves usually shorter than those of the sterile shoots, opposite and decussate, with sheaths formed by the fusion of the two petioles; with 2 lines of hairs continued down the stem below the sheaths. The uppermost pair of leaves more spiny at the base, connate but not sheathing. Bracts ovate, spinose or ciliate, concave or folded. Inflorescence $\pm$ spherical, sometimes with one or two separated clusters below the primary head. Involucel cylindrical - campanulate, membranous at first becoming coriaceous in fruit, with short, often reflexed hairs inside, $0 \cdot 5-1 \cdot 5 \mathrm{~mm}$ below the rim, with $9-15$ (or rarely more) setae, $\pm$ equal in length and with numerous hairs around the rim. Calyx $\pm$ cylindrical, mouth obliquely cut, usually with 2 lateral and 3 posterior teeth, the latter sometimes connate and with 1,3 or more spines, the lateral teeth often spiny with 0 -several setae. Calyx teeth (9-) $11-12.5(-14) \mathrm{mm}$, the tube $4-6.5 \mathrm{~mm}$ with crisp hairs on the edge and sometimes also a few inside below the posterior teeth, rarely to the base. Corolla pink, or purplish, curved, the tube $(1 \cdot 4-) 1 \cdot 8-2 \cdot 1 \mathrm{~mm}$ wide, slightly swollen below the mouth with whitish spreading hairs all round. Lobes of the limb spreading, 5 , subequal, the lower 3 rather broader than the upper 2, the middle lower lobe slightly broader than the 2 laterals. Stamens 4 , all fertile, anthers introrse, subequal, scarcely emergent from the corolla tube, 2 inserted at the base of the swelling, the other 2 slightly lower. Stigma disc-shaped, scarcely papillose at the edge; style thread-like with a tuft of hairs just below the stigma. Ovary glabrous or rarely with a few long hairs, unilocular, with a pendulous ovule. Achenes rugose.

Distribution and ecology: A. nepalensis is the most commonly collected species in Nepal, Sikkim, Bhutan, and southern Xizang. There are fewer records to the east of Lhasa and in its immediate district, and it is thinly spread in Yunnan and Sichuan. In common with the majority of species in the Morinaceae, A. nepalensis is a plant of high altitudes and has been recorded at altitudes between 2500 and 4900 m , although the majority of records are in the ranges $3250-4750$ m . It is recorded from a wide range of habitats, from rock ledges, alpine meadows, and dry slopes to woodland, and is often described as being abundant in the places where it occurs. The flowering season is mainly from June to July, but plants have been observed flowering as early as May and occasionally as late as in August, September, and October.

## 2. Acanthocalyx delavayi (Franchet) M. Cannon, comb. nov.

Morina delavayi Franchet in Bull. Soc. bot. Fr. 32: 9 (1885). Type: In monte Hee Chan-men prope Lankong, 2.6.1884, Delavay 52 (P-holotype).
Morina bulleyana Forrest \& Diels in Notes R. bot. Gdn Edinb. 5: 208 (1912). Type: Chung Tien Plateau, $3400-3600 \mathrm{~m}, 1904$, Forrest (E-lectotype). Mountains near Tali [Mt. Tsang Chan], 20.6.1884, Delavay 90 ( P - isotype).
Barleria crotalaria A. Léveillé in Reprium Spec. nov. Regni veg. 12: 285 (1913). - Lauener in Notes R. bot.


Fig. 4 Acanthocalyx nepalensis (D.Don) M. Cannon - the type species and a typical member of the genus Acanthocalyx.

Gdn. Edinb. 32: 116 (1972). Type: Tong tchouan, Yunnan, 2700 m , Maire s.n. and Lou Pou, Yunnan, $3000 \mathrm{~m},-.7 .1912$, Maire s.n. (E-syntypes).
Low perennial herbs, with short woody rhizome, covered with remains of old leaf bases. Leaves of sterile shoots entire, linear-lanceolate to ovate-lanceolate, slightly spiny or spineless, up to 16 $\times 3 \cdot 2 \mathrm{~cm}$, fusing to form pale coloured sheaths. Fertile shoots erect, 10-35 (-45) cm, lowest pair of leaves ovate, with the sheath equalling or exceeding the lamina. Lower leaves spiny or $\pm$ spineless. Upper stem leaves ovate-lanceolate to broadly ovate, deep green above, somewhat glaucous below, with 3-5 parallel veins, the petioles connate or sheathing, with 2 rows of white hairs continuing down the stem from the join. Bracts broadly ovate, the edges spiny, becoming more spiny towards the base. Inflorescence $\pm$ spherical, sometimes with a few flowers in the axils of the uppermost pairs of leaves. Involucel cylindrical-campanulate, fragile, papery at first, becoming thicker and larger in fruit, teeth $\pm$ uniform in length (16-) $20-30$, hairy inside the top $0.5-1.5 \mathrm{~mm}$, rarely to the base, very rarely without hairs. Calyx tube cylindrical-campanulate, (7.5) 9-13 ( -15 ) mm, mouth obliquely cut, usually with 2 lateral and 3 posterior teeth, sometimes deeply cut, rarely quite entire, or the whole limb entire, terminating in a spine, the outside usually glabrous, rarely with a few hairs at the tip. Corolla magenta, red-crimson or purple, tube broad (2-) $2.5-4.5 \mathrm{~mm}$, straight or $\pm$ curved below the region of the swelling, sparsely hairy to glabrous below and sparsely hairy to hairy above; lobes of the limb $3 \cdot 5-6 \mathrm{~mm}$. Stamens 4, all fertile, the anthers introrse, the lobes subequal, scarcely emergent from the corolla tube, 2 inserted at the base of the swelling, 2 just below. Stigma disc-shaped, somewhat papillose at the edge. Style thread-like, with a tuft of hairs just below the stigma. Ovary pubescent. Achenes rugose.

Observations: The syntypes of Barleria crotalaria A. Léveillé have glabrous ovaries and are somewhat intermediate between $A$. delavay i and $A$. nepalensis.

Distribution and ecology: A. delavayi occurs in western China, mainly in Yunnan and Sichuan, spreading northwards into Gansu and into the Xizang-Burma border region. It is a plant of high altitudes and has been collected between 2500 and 4000 m . Collectors record it from a variety of habitats, from dry stony ground to glacier meadows and the edges of pine woods. It appears to flower a little earlier than A. nepalensis, with the majority of records for May and June, with one single example from April and a few from July to October. However, the earlier flowering span may be merely a reflection of the somewhat lower altitudinal range.

## 3. Acanthocalyx alba (Hand.-Mazz.) M. Cannon, comb. nov.

Morina alba Hand.-Mazz. in Sber. Akad. Wiss. Wien, Math.-Nat. 62: 68 (1925). Type: Likiang, Yulung Shan, N.W. Yunnan, $3500-4000 \mathrm{~m}, 1914$, Handel-Mazzetti 3799 (?W - not seen).
Morina leucoblephara Hand.-Mazz. in Sber. Akad. Wiss. Wien, Math.-Nat. 62: 68 (1925). Type: Yunnan, 1914, Handel-Mazzetti 3536 (?W - not seen).
Low perennial herbs, with short woody rhizome, covered with remains of old leaf bases. Leaves of the sterile shoots entire, linear-lanceolate, rarely slightly ovate-lanceolate, with short hairs on the margins, with or without spinose setae, lamina glabrous above and below. Fertile shoots erect, 20-35 (rarely to 45) cm, lowest pair of leaves ovate, thinly coriaceous, deeply sheathing, usually spineless, the sheaths as long as or longer than the lamina. Upper stem leaves entire, opposite and decussate, linear to linear-lanceolate, green above, somewhat glaucous below, 3-5 veined, the sheaths becoming shorter near the top of the stem, with 2 lines of white hairs below the fusion point of the petioles. Uppermost pair of leaves linear-lanceolate, slightly sheathing or connate. Bracts broadly ovate, spinose, very prickly at the base. Inflorescence $\pm$ spherical, sometimes with one extra whorl in the axils of the uppermost pair of leaves. Involucel cylindrical - campanulate, persistent and enlarging in fruit, teeth 14-16(-17), glabrous or with a few hairs on the veins within the tube, with numerous hairs on the rim. Calyx tube cylindrical, $1-2 \cdot 5 \mathrm{~mm}$, mouth obliquely cut, limb (5-) 6-7 (-12) times as long as the tube, with 3 posterior teeth and 2 lateral, sometimes deeply cut and sometimes spiny. Corolla usually white, cream or yellowish, or shading to puce, the tube markedly curved, very hairy above, with few to 0 hairs below. Tube
$12-20 \times 1.1-1.7 \mathrm{~mm}$, limb 5-lobed as in A. nepalensis. Stamens and stigma and style as in A. nepalensis. Ovary pubescent. Achenes pubescent, at least when young, often at maturity somewhat rugose.

Observations: Flower colour varies considerably. Ludlow \& Sherriff 5017 records the colour as creamy-yellow, ranging to puce. This seems to correspond to a number of gatherings by several collectors who label their specimens as having white flowers, but in the gathering include individuals which appear to have much darker flowers than the average for the sample. The calyx is often flushed or almost completely coloured purple, both in the deep coloured specimens and in those with obviously white flowers.

In his review of Chinese Morina species, Pai (1938) includes Morina leucoblephara as a distinct species. Three gatherings recognised by him as M. leucoblephara have been seen by us (Kingdon Ward 5894, Dungboo 4634 and Forrest 28444) and appear to be identical in all respects to Acanthocalyx alba apart from their smaller stature. Handel-Mazzetti (1925) separates Morina leucoblephara from M. alba by size, the deep ventral fissure of the calyx and the 3 posterior teeth of the calyx, said to be totally connate in M. leucoblephara. Examination of the calyces of many plants of all Acanthocalyx species shows a great variety in the depth of the three posterior teeth; even in one plant there may be 3 or 5 deeply cut teeth, 3 closely connate teeth, or only one single tooth. There seems therefore to be no recognisable distribution pattern of this character in the populations. The depth of the ventral fissures in the Forrest specimen is 1.5 mm , which is within the range shown by many of the $A$. alba specimens measured by us.

Distribution and ecology: A. alba has a similar distribution to $A$. delavayi, occurring in Gansu, Sichuan, and Yunnan, but it does not extend so far to the west as that species. One specimen has been seen from northern Assam and one from eastern Xizang. A. alba is also a high altitude plant and has been collected from $2500-4250 \mathrm{~m}$. It is noted as being abundant or extremely common by a number of collectors who describe it as a plant of varied habitats from open, dry pine forests to alpine meadows or even swamps. It flowers mainly between June and August, with occasional records from May and October.

## II. CRYPTOTHLADIA (Bunge) M. Cannon, stat. nov.

Morina Section Cryptothladia Bunge, Beit. Kentniss Flor. Russlands: 321 (1852).
Type species: Cryptothaldia parviflora (Karelin \& Kir.) M. Cannon
Plants perennial, often tufted, with a woody rhizome covered with the fibrous remains of previous year's leaves. Leaves linear to lanceolate, whorled or rarely paired, the margins often irregularly sinuate dentate and very spiny. Inflorescence verticillate, with several to many verticillasters, flowers sessile or short stalked; sometimes flowering at ground level and subsequently elongating to full height. Bracts free, connate at the base or fused for up to half of their length, forming shallow cups. Involucel tubular to campanulate, enlarging and becoming more rigid in fruit, with few to numerous teeth. Calyx cylindrical to campanulate, 2-lipped, each lip 2- (or rarely more) lobed. Corolla tubular, scarcely emergent from the calyx, 4- (or scarcely 5) lobed, rarely 2 -lobed, the upper lip entire or scarcely 2-lobed, the lower lip often with 1 large central lobe and 2 much smaller lateral lobes; the lips scarcely separating and the flowers probably cleistogamous. Fertile stamens 2, inserted halfway down the corolla tube (one-third of the way in C. chinensis), anthers introrse, subequal. Pollen yellow or rarely purple-violet. Sterile stamens 2 , inserted at or near the base of the corolla tube ( $1 / 3$ of the way up in C. chinensis), sterile anther lobes equalling or exceeding the fertile anther lobes. Nectaries 2 , at the base of the corolla tube, at or below the insertion of the sterile stamens. Style a little shorter than the corolla tube or just equalling it. Ovary unilocular, ovule solitary, pendulous. Achenes rugose, with obliquely truncate apex.

Six species of Cryptothladia are recognised by us: C. parviflora from the Tian Shan and Pamirs of south-east U.S.S.R. and its borders with China, C. polyphylla from south of the Himalayas, mainly in Nepal, but also occurring in Bhutan and south-eastern Xizang, C. kokonorica from north of the Himalayas in Xizang, C. chinensis from north-western China, C. chlorantha

occurring to the south of the range of $C$. chinensis in China, and C. ludlowii from Xizang, Assam, and Bhutan. See Fig. 5.

## Key to the species

1a. Bracts connate, forming shallow cups throughout the inflorescence, teeth of the involucel much shorter than the tube ( $1 / 2$ as long or less) 5. C. polyphylla (p. 20)
1b. Bracts free (fused at the top of the inflorescence in C. parviflora), teeth of the involucel at least $2 / 3$ as long as the tube: ..... 2
2a. Leaves entire or nearly so: ..... 2
3a. Bracts softly leafy with long acuminate tips, lower stem leaves not sheathing
4. C. chlorantha (p. 19)
3b. Bracts small, tri-lobed, or irregularly palmate-dentate, lower leaves deeply sheathing ..... 6. C. Iudlowii (p. 22)
2b. Leaves coarsely sinuate-dentate: ..... 4
4a. Bracts connate in the upper whorls 2. C. parviflora (p. 18)
4b. Bracts not connate in upper whorls: ..... 5
5. Staminodes $1 / 3$ of way up corolla tube, calyx lobes 4 , shallowly notched (up to 1 mm )1. C. chinensis (p. 17)
5. Staminodes at base of corolla tube, calyx lobes 5 (rarely 4), deeply notched (up to 7 mm )
3. C. kokonorica (p. 19)

## 1. Cryptothladia chinensis (Pai) M. Cannon, comb. nov.

Morina chinensis Pai in Reprium Spec. nov. Regni veg. 44: 122 (1938). Type: Tao river basin in meadows of Maerhku, 2700-3000 m, 25.7.1925, Rock 12952 (E; K - lectotype).
Morina parviflora var. chinensis Batalin - referred to by Diels in Notes R. bot. Gdn Edinb. 5: 208 (1912)nom. nud.?
Herbs, with short rhizomes covered with old $\pm$ complete leaf bases. Lower stem leaves up to 10 $(20) \times 8(12) \mathrm{cm}$, whorled or paired, linear in outline, irregularly sinuose, spinose-dentate; the teeth 2-3 fid with triangular lobules and apical spines and longer retrorse basal spines; the petioles fused to form loose sheaths, glabrous. Upper stem leaves similar but smaller, up to 6 in a whorl, free or scarcely connate, rarely with a very short sheath. Flowering stems up to 50 cm with 4 rows of hairs in upper parts, bearing several somewhat separated whorls of up to 20 flowers; the stem visible between at least the lower whorls. Bracts leafy, free, up to 25 mm , the lower part broadly ovate, markedly whitish and strongly net-veined; apices narrowly acuminate, spiny, greenish, the blade spinose-dentate with many longer and often retrorse spines at the base, hairy below and on the margin. Involucel narrowly campanulate to cylindrical, villous outside, tube 6-8 mm with $9-12$ irregular spiny teeth (teeth not laminate at the base), often exceeding the calyx, 4-5 mm, 3 or 4 teeth often longer than the rest. Calyx $6-8 \mathrm{~mm}$, cylindrical, with a 2 -lobed limb, the lobes shortly bifid, the lobules slightly rounded or cuspidate, tube $3-4 \mathrm{~mm}$ with few hairs outside, villous and glandular within. Corolla cylindrical, the throat somewhat swollen, scarcely visible within the calyx lobes, limb more or less 2-lipped; lower lobe with 2 very small lateral lobes, upper lobe entire or rarely slightly divided; lips scarcely open at anthesis, pubescent and with sessile and stalked glands both within and without. Fertile stamens borne $2 / 3$ of the way up the corolla tube, filaments short with a tuft of hairs just below the anthers. Anther lobes unequal, one up to 1.5 times as long as the other. Sterile stamens with short filaments and lobes as long as those of the fertile stamens, borne $1 / 3$ of the way up the corolla tube, with 2 glandular nectaries at the base of the tube. Style about as long as the corolla, stigma disc-shaped. Mature achenes surrounded by the enlarged involucel and surmounted by the enlarged calyx; $3-4 \times 2-2.5 \mathrm{~mm}$, plano-convex, furrowed on the abaxial face, the top edge of the adaxial side rounded, smooth, not crenate.

Observations: The flowers are referred to as green on the labels of two specimens collected by Rock. This may refer to the colour of the calyx, as the corolla is scarcely noticeable within the more conspicuous calyx. Herbarium specimens appear to have whitish corollas.

A specimen collected at Sungpan hsein in Sichuan (Fang 4270) is probably best placed here. It obviously has affinities with a specimen for which the collector's name cannot be transliterated 4484, which is similar in many respects to C. parviflora, but the shape of the calyx lobes is much more like those of $C$. chinensis, as are the achenes.

Distribution and ecology: C. chinensis is a high altitude plant; most collections are from localities at $3000-4000 \mathrm{~m}$. It occurs in China in Xizang, Sichuan, Gansu, and Quinghai. Its habitats are variously noted as alpine meadows, mountain tops, and roadsides, flowering in June and July.

## 2. Cryptothladia parviflora (Karelin \& Kir.) M. Cannon, comb. nov.

Morina parviflora Karelin \& Kir. in Bull. Soc. Nat. Moscou 15: 373 (1842). Type: Alpis Alatau ad sinistram ripam fl. Sarchan jacentis, Karelin \& Kirilow (LE, not seen).
Herbs forming dense tufts, with sterile and fertile shoots. Rhizomes and lower parts of stems covered with fibrous sheathing bases from old leaves. Lower stem leaves and leaves of sterile shoots glabrous, linear with irregularly cut inciso-dentate spiny margins, up to $15 \times 1 \mathrm{~cm}$, in whorls of up to 6; petioles expanding abruptly into broad, fused bases. Upper stem leaves similar to those of sterile shoots, very shortly sheathing or barely connate, the uppermost whorl free; covered with spreading crisped hairs, with stalked and sessile glands on the upper surface, especially on the margins, the lower surface with fewer hairs and glands. Flowering stems up to 35 cm when mature, but very short at first and elongating during flowering; ridged and glabrous below, thickly covered with spreading hairs and glands above, square in section between the whorls of flowers, which are separate below but confluent above. Bracts up to 20 mm , free in the lower whorls, connate or fused above; the bases broadly ovate and conspicuously net-veined, the apices spiny, narrowly acuminate with long, narrowly-triangular spiny teeth densely covered with spreading hairs and glands on the upper surface, fewer below. Involucel cylindrical to campanulate, villous and with occasional stalked glands at anthesis, tube 5 mm , with 4-5 broad-based laminate teeth; 2 teeth subequal, c. 4 mm , much longer than the others and becoming rigid and spiny when mature. Calyx $\pm$ campanulate, conspicuously net-veined, villous and glandular, limb 2-lipped, each lip deeply bifid, lobes acute, sometimes spiny tipped. Corolla pinkish, cylindrical, the throat somewhat swollen, just emergent between the calyx lobes; with 4-5 fimbriate lobes, the upper lip emarginate or bilobed, the middle lobe of the lower lip $\pm$ equalling the lateral lobes. Fertile stamens 2, borne halfway up the corolla tube, anther lobes subequal, the shorter about $2 / 3$ the length of the longer; filaments villous or with a tuft of spreading hairs. Sterile stamens borne just above the base of the corolla tube, less than $1 / 3$ from the base; sterile anther lobes longer than the lobes of the fertile anthers, very narrow, somewhat pigmented. Nectaries lobed, at the base of the corolla, extending upwards as far as the base of the filaments of the sterile stamens. Style about as long as the corolla tube, stigma disc-shaped. Mature achenes $6 \times 4 \mathrm{~mm}$, rugose, shallowly furrowed and slightly convex on the abaxial face, the apex obliquely truncate, tapering to an acute point.

Observations: The fruiting specimen 4484 (collector's name not readable) on loan to us from Peking is in habit very much like C. chinensis, especially the specimen Fang 4270 . However, the calyx lobes are acute, and the seed is much larger than that of typical C. chinensis. Pai considered it to be Morina kokonorica (= Cryptothladia kokonorica), but it has only four calyx lobes, and the plant is less spiny and the whorls of flowers are more separated than those of any specimen we have seen of C. kokonorica. It corresponds to C. parviflora in seed, habit, and the shape of the calyx lobes, and for these reasons we prefer to place it here. It has not been possible to translate the blurred chinese characters on the label. The superficial similarity of this specimen with C. chinensis may explain, in part, early references to Morina chinensis as a variety of $M$. parviflora, but apparently without valid publication.

Distribution and ecology: This species is known from Turkestan, from the borders of Kazakhstan with China (Dzungariau Ala-Tau), and from Kirgizia. It is stated to occur in the
alpine zone between $3000-4000 \mathrm{~m}$, and to flower in June. Some collectors mention an unpleasant odour, reminiscent of some Labiateae.

## 3. Cryptothladia kokonorica (Hao) M. Cannon, comb. nov.

Morina kokonorica Hao in Reprium Spec. nov. Regni veg. 40: 215 (1936). Type: Kokonor in den
Wustentalern, 12.9.1930, Hao 1268 (not seen).
Herbs forming tufts from short woody rhizomes densely covered with the fibrous remains of old leaf bases. Lower stem leaves and leaves of sterile shoots paired or whorled, linear, coarsely and irregularly sinuate-dentate, with broadly triangular spinose lobes, and with broad petioles fused to form sheathing bases. Upper stem leaves similar, 5 or more whorled, up to $20 \times 1 \mathrm{~cm}$, free or scarcely connate, with numerous retrorse and erect spines at the leaf base, sessile. Flowering stems up to 40 cm , ridged and with 4 rows of hairs in the furrows above, terete and glabrous below, bearing up to 7 whorls of 16-20 flowers, the stem becoming visible at least between the lower whorls after flowering. Bracts $7-8$ whorled, very spiny, often recurved and folded, becoming very stiff after flowering; coarsely toothed and with short stiff yellowish spines, broadly ovate at the base with a long acuminate spiny tip, glabrous. Involucel cylindricalcampanulate, tube $5-7 \mathrm{~mm}$, often with 16-18 teeth, 2(3-4) teeth much larger than the rest, often with several lateral spines or teeth, the longest as long as or exceeding the calyx. Calyx tube 4-5 mm with few hairs; limb 2-lobed, each of which is very deeply divided almost to the tube, to form (4) 5 (or rarely more) subequal lobes; the lobes ovate, acute to acuminate and often spiny tipped, greenish and leafy at anthesis, becoming dry and spiny with inrolled edges in fruit, and with a conspicuous tuft of hairs at the base of the tube. Corolla much shorter than the calyx,$\pm$ cylindrical with a few very short hairs on the outside; 4-lobed, the mouth scarcely opening. Fertile stamens borne halfway up the corolla tube, with short filaments, anthers subequal. Sterile stamens stalked, at the base of the corolla tube, with a nectary at the base of the filaments. Style nearly equalling corolla tube, stigma disc-shaped. Mature achenes rugose; convex on the adaxial face concave and deeply furrowed on the abaxial face; apex obliquely truncate, tapering to an acute point, $5.5 \times 3-3.5 \mathrm{~mm}$.

Observations: One gathering at BM (Richardson 124) consists of very small, low-growing plants, while others show individuals of varying heights. It seems probable that, in common with many other alpine plants, this species may begin flowering very close to the ground, after which the inflorescence elongates very rapidly to reach its maximum height, while flowers are still present in the upper part of the inflorescence. Several collectors describe the corolla colour as white.

Distribution and ecology: C. kokonorica is a high altitude species and collections seen range from $3750-4725 \mathrm{~m}$. All specimens seen by us are from Xizang, but the type locality is from Kokonor in Quinghai. Its habitat has been recorded as stony ground and open hillsides, where it flowers in June and July.

## 4. Cryptothladia chlorantha (Diels) M. Cannon, comb. nov.

Morina chlorantha Diels in Notes R. bot. Gdn Edinb. 5: 208 (1912). Type: East flank of Lichiang Range, Yunnan, 3000-3300 m, -.6.1906, Forrest 2482 (E - holotype; K - isotype).
Morina chlorantha var. subintegra Pax \& K. Hoffm. ex Limpr. in Beih. Repert. Spec. nov. Regni veg. 12: 497 (1922). Type: Ost. - Tibet, Ta Tsien lu, Sheto, steinige Halden des Tales vor dem Laniba, 4000 m , Limprict 1834; Ta tsien lu, Dawo, Gata, auf den Grassmatten des Passes Hai tse schan am Dshava, 4350 m, Limprict 1899 (not seen).

Herbs with stout rhizomes densely covered with remains of old leaf bases. Lower stem leaves ovate to obovate, $13-25 \times 2 \cdot 5-4 \mathrm{~cm}$, somewhat toothed, especially near the base of the stem, with short spines around the edge; gradually tapering into petioles which become joined to form sheaths round the lower part of the stem, glabrous. Upper stem leaves entire, whorled, not connate; sessile, lanceolate or broadly lanceolate, sometimes with small spines. Flowering stems
$35-50 \mathrm{~cm}$, hairy all round above, glabrous and somewhat ridged below, bearing up to 7 somewhat separated whorls of 12-20 flowers, the stem often visible between the whorls. Bracts softly leafy in whorls of (3-) 4(-6), not connate, spreading and occasionally slightly recurved, broadly ovate, tapering gradually into a long-acuminate leafy tip or into a short spine, usually hairy on the margin and below. Involucels cylindrical campanulate, densely covered with hairs and sessile and stalked glands, with 11-14 spiny teeth, the bases only rarely laminate, slightly shorter than the tube, exceeding the corolla. Calyx, 8-11 mm, tube cylindrical 2.5-4 mm, with hairs and sessile and stalked glands more numerous within than without; with a 2 -lobed limb, each lobe deeply notched, the lobules with rounded or spiny tips. Corolla hidden within the calyx lobes, white, cylindrical, with a somewhat swollen throat and with numerous hairs and sessile and stalked glands; 2-lipped, the lower lip with a large central lobe and 2 much smaller laterals, the upper lip $\pm$ entire or shallowly 2-lobed, the lobes shallowly crenate, the lips scarcely separating at anthesis. Fertile stamens borne halfway up the corolla tube, anther lobes very unequal, one sometimes twice the length of the other. Sterile stamens at the base of the tube, with short filaments, and lobes as long as those of the fertile stamens, and irregularly lobed nectaries at the base of the filaments of the sterile stamens. Style equalling corolla tube, stigma disc-shaped. Mature achenes surrounded by the enlarged involucels and surmounted by the enlarged calyx, $5 \times 4 \mathrm{~mm}$; subglobular, convex on the abaxial face, scarcely furrowed, the apex somewhat obliquely truncate, the top edge obtuse, entire or slightly crenate.

Distribution and ecology: C. chlorantha is distributed in Sichuan and Yunnan to the south of the range of $C$. chinensis. It occurs in alpine meadows, grassland, and on moist shady cliff ledges at altitudes between 3000 and 4425 m . It is in flower between May and July and is described as having a rank odour.

## 5. Cryptothladia polyphylla (Wallich ex DC.) M. Cannon, comb. nov.

Fig. 6.

Morina polyphylla Wallich ex DC., Prod. 4: 644 (1830). Type: Nepal, Gossain Than, Wallich 425 (BM; K; LE-type collection).

Tufted herbs, the rhizome thickly covered with the fibrous remains of several previous years' leaf bases. Lower stem leaves whorled, with long narrow petioles fused to form sheaths at least $1 / 3$ the length of the lamina, rarely equalling it, linear to linear-lanceolate, up to $40 \times 1 \cdot 5-2(-3 \cdot 5) \mathrm{cm}$, very coarsely incisodentate with 3-5 fid, broadly based triangular lobules with apical spines, glabrous or slightly pubescent. Upper stem leaves in whorls of (3-) 4-6, similar to the lower, but smaller, the bases much less deeply sheathing, rarely almost free. Flowering stems up to 45 cm , terete or slightly furrowed, with numerous spreading whitish hairs above, glabrous below, bearing several whorls of up to 16 sessile or short stalked flowers in a dense cylindrical spike, the lowest whorl rarely slightly separated from the rest. Bracts in whorls of (3-) 4-6, deeply connate at the base forming a pale cup-shaped structure with conspicuous green net-veining, the free tips of the bracts greenish, linear, with lateral spines tapering to a robust often yellowish spine. Involucel (6-) $9-13 \mathrm{~mm}$, shorter than the corolla, but becoming larger and more rigid in fruit; cylindrical, toothed, usually pilose, rarely nearly glabrous; with many sessile and a few stalked glands; teeth $8-10$ or fewer, $1-3 \mathrm{~mm}$ at anthesis, with a broad laminate base, tapering to a terminal bristle or spine, 1 or 2 longer than the rest. Calyx cylindrical to campanulate, $7-12 \mathrm{~mm}$, tube 4-5 mm, usually very pilose and glandular within; limb expanded with 2 spreading white or lavender lobes, each deeply divided for at least half of its length, apices usually rounded, rarely, spiny tipped. Corolla just visible within the calyx lobes, pink or white, equalling the involucel, $\pm$ cylindrical with 4-lobed scarcely expanded limb, the lips scarcely opening, dentate-fibrillate at the edges. Fertile stamens 2, borne halfway up the corolla tube, anthers introrse, lobes subequal. Pollen purple violet. Sterile stamens at base of corolla tube, short-stalked, lobes long and tapering to a point, violet coloured, with a 3-lobed nectary at the base of each. Style equalling the corolla tube, stigma disc-shaped. Mature achenes $4.75-5.5 \times 2.75-3 \mathrm{~mm}$, plano-convex, obliquely truncate, the top edge of the adaxial face obtuse, crenate, scarcely furrowed on the


Fig. 6 Cryptothladia polyphylla (Wallich ex DC.) M. Cannon - a typical member of the genus Cryptothladia.
abaxial face, surrounded by the rigid expanded involucel and surmounted by the enlarged calyx.
Observations: The colour of the inflorescence has been variously described by collectors. Most describe the 'flowers' as red, bluish-red, pink, white, or pale violet. As the corolla is so small it is likely that it has been overlooked in a number of cases. In the specimens examined by us the young flowers are generally much paler in colour than the mature ones. It seems very probable that, as in the more familiar Morina longifolia and M. persica, the corolla changes colour from white to deep red as it matures. The calyx is described as pale green or white, the bracts being white or with pink margins. Many references to 'flower colour' probably refer to the conspicuous calyx rather than the corolla. The whole plant is recorded as having an unpleasant smell when bruised, and the leaves as being 'strongly aromatic'.

Distribution and ecology: C. polyphylla has been collected mainly from Nepal, with a few records from Bhutan, and two from the southernmost part of Xizang. It ranges in altitude from 2600 m to 4700 m . The flowering period appears to be mainly June and July, but it may extend from April to September. It is recorded as being abundant in some localities and appears to prefer a variety of mostly open habitats, such as grassy hill-slopes, alpine meadows and the like, although it has been collected from 'the forest floor' at 2600 m , which must be near the lower limit of its altitudinal range.

## 6. Cryptothladia ludlowii M. Cannon, sp. nov.

Fig. 7.
Ab aliis speciebus Cryptothladiae spica cylindrica et densa, bracteis trilobis differt.
Herbae caespitosae, caulibus floriferis anthesis initio brevibus tum celeriter per anthesis ad 47 cm altis extendentibus. Folia lanceolata, 4-verticillata, integra vel paucidentata; petioli generatim connati vaginas laxas facientes, eas caulis basi profundissimas eas super minores, petioli supremitamen vix connati. Spika densiflora, cylindrica verticillis 20 ut minimum, in quoque 8-12 floribus. Bracteae parvae, imbricatae, saepe rubrae, verticillo infimo lanceolato superioribus trilobis, lobis spinoso-dentatis medio eis lateralibus maiore, apicibus acutis vel cuspidatis. Involucellum dentibus 4-8 (raro-12) uno quam ceteris saepe longiore latioreque, basi laterali, laminaribus anthesis initio mollibus et fragilibus, grandioribus rigidisque in maturitate. Limbus calycis bifidus, lobis breviter bifidis, lobulorum apicibus obtusis vel cuspidatis. Corolla parva, quadriloba, lobo posteriore fimbriato, anteriore integro super posteriorem arcuato. Stamina fecunda 2, medio corollae tubo inserta; staminodia imo inserta, lobis sterilis eos staminum fecundorum aequantibus vel superantibus. Achenia parva, $3 \times 1.75 \mathrm{~mm}$. subglobosa.

Type: Bhutan, Ju La, Mangbe Chu, 4250 m., Ludlow, Sherriff \& Hicks 16903 (BM - holotypus; E isotypus).
Herbs, the stem base and top part of the rhizome thickly covered with the fibres of old leaf bases. Lower stem leaves and leaves of the sterile shoots, in whorls of 4, lanceolate, entire or slightly toothed, with rather broad petioles fused together into loose sheaths, $5-7.5 \times 10-12 \mathrm{~mm}$, the margins with hairs and short spines, slightly glandular - pubescent above. Upper stem leaves similar to the lower, with broad based petioles forming shallower sheaths, the uppermost whorl often barely connate. Flowering stems very short at first, $2-3 \mathrm{~cm}$, elongating rapidly up to 47 cm , terete or slightly grooved, densely covered with whitish, spreading, mostly retrose hairs. Inflorescence cylindrical, dense, up to 20 cm , often with 20 or more close packed whorls, 8-12 flowers in each whorl. Bracts small, leafy, regularly opposite and decussate, imbricate, lowest whorl rather similar to leaves but smaller; usually 3-lobed, lobes irregularly spinose-dentate, acute or cuspidate, the centre lobe larger than the laterals, often reddish or deeply coloured. Involucel campanulate - cylindrical, pilose, often with stalked or sessile glands; teeth 4-8(-12), one often larger than the others, broad at the base, laminate, soft and fragile at anthesis, becoming larger and rigid in fruit. Calyx tube cylindrical-campanulate, $2 \cdot 5-4 \mathrm{~mm}$ at anthesis; limb bifid, the lobes shallowly divided, lobules rounded to apiculate, glabrous without, with long white hairs and glands within. Corolla scarcely visible within lips of the calyx, $\pm$ cylindrical with a scarcely enlarged throat, glabrous without, 4-lobed, the posterior lobe $\pm$ fimbriate, the anterior lobe entire, markedly exceeding the posterior and arched over it, with strong erect hairs on the inner surface, with 2 very small lateral lobes; the whole closed or scarcely separating at


Fig. 7 Holotype specimen of Cryptothladia ludlowii M. Cannon.
anthesis. Fertile stamens 2, with short filaments, borne halfway down the corolla tube, anther lobes subequal, filaments with a tuft of hairs below the anthers. Sterile stamens 2, at the base of the corolla tube, shortly stalked, deeply pigmented, the sterile anther lobes as long as or longer than those of the fertile anthers, nectaries irregularly lobed, at the base of each sterile stamen. Style a little shorter than corolla tube, stigma disc-shaped. Mature achenes $3 \times 1.75 \mathrm{~mm}$, subglobular, with a shallow furrow on the abaxial face, apex slightly obliquely truncate, obtusely pointed, somewhat rugose.

Observations: We take particular pleasure in naming this species after the late Frank Ludlow, Honorary Associate of our Department, who was for many years an outstanding specialist on Himalayan plants and who, with George Sherriff, made many important collections in this region. A specimen from Bhutan Gould 486 (K) has a few long, narrow, spiny tipped bracts at the base of the inflorescence, becoming smaller and similar to those of typical C. ludlowii towards the apex. It closely resembles $C$. ludlowii in all other respects.

Distribution and ecology: C. ludlowii has been collected at altitudes of $3500-4250 \mathrm{~m}$ in Bhutan and its borders with Xizang and Assam. It is reported from a variety of habitats, such as amongst shrubs, on rocky hillsides, and on cliff ledges. Flowering is from May to September. The flowers are described as yellow, or yellowish green, but some obviously also have a red or violet pigment. The flowers are said to be sweet scented.
Specimens seen: Bhutan: Ju La, Mangbe Chu, 4250 m, 19.7.1949, Ludlow, Sherriff \& Hicks 16903 (BM holotype; E - isotype); Me La, south side, $4250 \mathrm{~m}, 29.5 .1949$, Ludlow, Sherriff \& Hicks 20305 (BM); Kantanang, Tsampa, $3850 \mathrm{~m}, 4.6 .1949$ Ludlow, Sherriff \& Hicks 19050 (BM; E); Ridge of Tashigong Kurted, 3700 m, 21.8.1915, Cooper 4525 (BM). Assam: Orka La, 4000-4250 m, 29.9.1938, Kingdon-Ward 14310 (BM). Xizang; Mago, 4000-4250 m, Kingdon-Ward 12383 (BM; K).

## III. MORINA L.

Morina L., Gen. Pl. ed.5: 16 (1754).
Asaphes Sprengel, Syst. Veg. 4 (2): 222 (1827), nom. superfl. (Art. 63.1).
Morina Section Diotocalyx DC., Prod.: 4: 644 (1830), excluding M. polyphylla Wallich ex DC.
Type species: Morina persica L .
Plants perennial with woody rhizomes, often covered with the remains of previous year's leaf bases. Leaves linear to oblong-lanceolate, spinose, incisodentate to almost entire, whorled or rarely paired, petioles often fusing to form loose sheaths. Inflorescence of several to many verticillasters, flowers sessile or short stalked. Bracts free, variable in size, usually spiny at least at the base. Involucel cylindrical to campanulate, with 8-16 teeth, 2 of which (usually opposite) are markedly longer than the rest. Calyx campanulate, with a 2 -lipped limb, the lips somewhat to deeply 2 lobed, persisting at least until the fruit is mature. Corolla with a long narrow tube and spreading into a $\pm 2$-lipped limb, the upper lip 2-lobed, the lower 3-lobed. Fertile stamens 2, adnate to the throat of the corolla; staminodes 2, cordate, within the corolla tube, Nectary 1, 3-lobed, anterior, at the base of the corolla tube. Style usually exceeding the stamens, stigma disc-like or slightly domed. Ovary unilocular, with a single pendulous ovule. Achenes rugose, somewhat or markedly obliquely truncate.

Four species of Morina are recognised by us: M. kokanica from the Tien Shan, M. coulteriana from the U.S.S.R., the western Himalayas, and Xizang, but absent from the eastern Himalayas, M. persica spreading from the Balkans through to the western Himalayas, and M. longifolia from the west and central Himalayas. See Fig. 8.

## Key to the species

1a. Leaves simple1. M. kokanica (p. 26)
1b. Leaves coarsely dentate-serrate:
2a. Corolla yellow, calyx lobes deeply notched2. M. coulteriana (p. 26)
2b. Corolla white or pink, calyx lobes entire or shallowly notched:
3a. Filaments 10 mm , teeth of involucel equalling or longer than the tube ..... 3. M. persica (p. 28)
3b. Filaments $1-2 \mathrm{~mm}$, teeth of involucel shorter than the tube 4. M. longifolia (p. 30)

2. Morina kokanica Regel in Bull. Soc. Nat. Moscou 40: 14 (1867). Type: Kokan, Turkestan, 1866, Sewerzow s.n. (LE, not seen).
Robust herbs with rosettes of sterile leaves and flowering shoots. Rhizomes woody, the top often covered with the fibrous remains of petioles from previous years leaves. Leaves of sterile shoots and lowest stem leaves glabrous, oblong lanceolate $25-35 \times 2-4.5 \mathrm{~cm}$, entire or rarely with occasional small teeth or prickles, midrib prominent, sometimes elongated to form a small spine; petioles free or fused to form short sheaths of $2-4 \mathrm{~mm}$. Upper stem leaves similar to lower, opposite or 3-4 whorled, petioles free. Flowering stems erect, somewhat square in section, grooved and ridged, glabrous below, with well-separated whorls of numerous short-stalked flowers; sometimes with short flowering shoots in the axils of the upper leaves. Bracts often rather leaf-like in the lowest whorl, broadly ovate with an acuminate tip tapering into a spine, the margin with a few rigid spines, somewhat villous below, the bases scarcely overlapping each other. Involucel cylindrical, the tube at anthesis $5-6 \times 3-4.5 \mathrm{~mm}$, becoming twicé as long or more at maturity, villous, with 12-16 teeth, two longer than the others, the longest shorter than the tube. Calyx cylindrical-campanulate, 5-6 $\times 3-4.5 \mathrm{~mm}$, often densely glandular hairy, limb $10-16 \mathrm{~mm}, 2-3$ times as long as the tube at anthesis, lobes shallowly bifid, tips obtuse. Corolla pale purple or pink with a darker area on the lower lip, the tube long and narrow, 35-45 $\times 1-3$ mm , the throat somewhat swollen, limb deeply cut, the lobes $10-15 \times 6-7 \mathrm{~mm}$, densely glandular hairy on the tube, somewhat less so on the interior and exterior of the limb. Fertile stamens 2, filaments about 7 mm , with a tuft of hairs just below the anthers, anther lobes subequal, the longer 2 mm , the shorter 1.7 mm . Staminodes 2 , minute, $\pm$ heart shaped, inserted $2-3 \mathrm{~mm}$ below the mouth of the corolla on the anterior side. Nectary 1,3-lobed, anterior at the base of the corolla tube. Style slightly exceeding the stamens, stigma disc-shaped. Achenes rugose, $\pm$ plano-convex with prominent diagonal veins, the apex obliquely truncate, somewhat fluted.

Distribution and ecology: M. kokanica is apparently confined to the Tien Shan and Pamir-Alai regions of Soviet central Asia at altitudes of $1600-3000 \mathrm{~m}$. The recorded flowering period is June to August.
2. Morina coulteriana Royle, Illus. Bot. Himal.: 245 (1835). Type: Kunawar, Royle s.n. (LIV holotype).
Fig. 9.
Morina breviflora Edgew. in Trans. Linn. Soc. Lond. 20: 62 (1846). Type: Pharkia near the Niti Pass in Kumaon, Edgeworth 259 (K - holotype).
Morina lehmanniana Bunge, Beit. Kenntniss Flor. Russlands: 321 (1852). Type: In den Alpen des Karatau, 12.9.1841, Lehmann s.n. (P, not seen).

Robust herbs with rosettes of sterile leaves and flowering stems. Rhizomes woody, often covered with old leaf bases. Leaves of sterile shoots and lower stem leaves $20-25 \times 2.5 \mathrm{~cm}$, glabrous, pinnatilobate, with spiny simple or compound teeth, petioles soft, fusing to form deep sheaths of $8-15 \mathrm{~mm}$. Upper stem leaves similar but smaller, in whorls of 3-4 ( -5 ), free or with short sheaths up to 3 mm or rarely more. Flowering stems erect, up to 1.25 m , stems ridged and glabrous below, square sectioned, villous and often deeply purple - pigmented above. Flowers in up to 7 whorls, the upper 2-5 whorls confluent, with 2-4 separated whorls below, flowers 50 or more per whorl, sessile in the outer part of the whorl, shortly petiolate (up to 2 mm ) nearest to the stem. Bracts broadly ovate with long acuminate tips, very spiny, often villous especially near the stem, conspicuously net veined. Involucel $\pm$ cylindrical, villous, $4-9 \times 2 \cdot 5-4 \mathrm{~mm}$, with $9-12$ teeth, 2 much longer than the others, the longest at least equalling or up to nearly twice as long as the tube at anthesis. Calyx glabrous to villous, with a large tuft of hairs at the base, glabrous or very shortly pubescent within, cylindrical-campanulate, 3-6.5 $\times 2-4 \mathrm{~mm}$, usually more than twice as long as wide at anthesis. Limb 2-lipped, villous, pubescent or glabrous without, glabrous within; lips deeply bifid for $2-5 \mathrm{~mm}$, apices acute or apiculate, with a short but prominent vein within, often extended beyond the tip to form a spine. Mature calyx often equalling the corolla


Fig. 9 Morina coulteriana Royle - a typical member of the genus Morina.
tube. Corolla yellow, tube villous, without glandular hairs or with very few, long and narrow, $25-30 \times 1-2 \mathrm{~mm}$, throat somewhat expanded, limb 2-lipped, the upper lip 2-lobed, the lower 3-lobed, median lobe of the lower lip $5 \cdot 5-10 \times 3 \cdot 5-6 \mathrm{~mm}$. Fertile stamens 2 , the filaments $2-3 \mathrm{~mm}$ at anthesis, inserted just within the corolla tube, with a tuft of long hairs below the anthers. Anther lobes unequal, one $2 / 3$ the length of the other. Staminodes minute, heart shaped, inserted $2 \cdot 5-4 \cdot 5 \mathrm{~mm}$ below the mouth of the corolla, below the anterior lip. Nectary 1, 3-lobed, anterior at the base of the corolla tube. Style slightly exceeding the stamens, stigma disc-shaped. Achenes with convex adaxial face, transversely rugose, abaxial face rugose, with very deep longitudinal furrows; apex somewhat obliquely truncate, with conspicuously undulate margins.

Observations: Plants from Xizang have slightly smaller corollas than those from the western end of the distribution range, the median lobe of the anterior lip of the corolla measuring 5•5-7 $\times 3-4 \mathrm{~mm}$, the width of the lateral lobes $2 \cdot 5-3 \mathrm{~mm}$, and the other lobes being correspondingly smaller than those of plants from further west. The length of the filaments also differ slightly, those of the Tibetan plants being slightly longer ( $2.75-3.5 \mathrm{~mm}$ ) than those of their western counterparts ( $2-2.5 \mathrm{~mm}$ ). A collection from Kashmir - Ludlow \& Sherriff 9123 from the Macchel Sapphire Mines, Kishtawar, has flowers similar in size to the Tibetan plants, but careful measurements of many individuals from both east and west show no other significant differences. No formal recognition of this variation therefore seems appropriate. A gathering from Kashmir - Robson 2013 consists of plants with rather narrow, almost spineless leaves, but corresponds to typical $M$. coulteriana in all other respects.

The type of M. lehmanniana has not been seen by us. It was described by Bobrov (1957) as from the upper Zaravshan, near the village of Fon and as being in the Paris Herbarium. A specimen from the Bunge herbarium from Zaravshan has been seen; it is identical in all respects with $M$. coulteriana. Specimens from this area tend to be conspicuously white-hairy above, but a number of Afghan and Kashmir plants also share this character.

Distribution and ecology: M. coulteriana occurs in the western Himalayas, the Hindu Kush, and central Afghanistan, and as far north as the Tien Shan, and also in eastern Xizang, but without intermediate stations in Nepal, Sikkim, or Bhutan. This kind of disjunct distribution has been referred to by several authors, e.g. Stainton (1972), Meusel (1971), and Kingdon-Ward (1936), and is shown by a large number of genera. In many cases such plants have been described as closely related vicarious species. In this instance, there seems to be no justification in recognising the Tibetan plants as a distinct taxon. It is improbable that the species occurs in intermediate Nepalese localities, as other similar species have been collected there and it seems likely that a yellow-flowered Morina would have readily attracted the attention of the many experienced collectors that have now travelled extensively in that country. There seems to be no obvious reason for its absence from the central Himalayas, since it is a species of open habitats and has been recorded from many substrates and habitats. It seems possible that the wetter monsoon conditions of the eastern Himalayas do not suit it so well, although it has been recorded as growing in a number of wet situations - streamside, wet sand, and moist pastures, and many arid habitats are available in Nepal behind the main range. It is a plant of high altitudes, rarely recorded below 2500 m and attaining 4000 m in Nepal; most records are found between $3000-3500 \mathrm{~m}$. Aitchison 746 from the Kurram Valley in Afghanistan has the fieldnote 'at and above $11000-13000 \mathrm{ft}(3300-4000 \mathrm{~m})$ this yellow flowered species quite replaces $M$. persica.' It has been reported from a wide range of habitats, both sheltered and exposed, possibly favouring dry conditions but also occurring in damp areas. The flowering period is mainly from June to August, with some plants still in flower in September.
3. Morina persica L., Sp. Pl. 1st ed.: 28 (1753). Type: Habitat in Persia ad Hispaham, Herb. Linn. 44/1 (LINN, isolated corolla only).
Morina orientalis Miller, Gard. Dict. 8th ed. (1768), nom. superfl. (Art. 63.1).
Morina verticillata Moench, Meth. Suppl.: 186 (1802), nom. superfl. (Art 63.1).
Morina wallichiana Royle, Illus. Bot. Himal.: 245, t. 55 (1835). Type: Mussooree, Royle (LIV - holotype).

Morina aucheri Jaub. \& Spach, Illustr. 5: t. 429 (1854). Type: Persia Australis, Aucher Eloy (BM; K) \& Kotschy ? 549 and 92190 (BM; K; LE - syntypes).
Morina graeca Jaub. \& Spach, Illustr. 5: t. 429 (1854). Type: Greece, Sibthorp s.n.; Bory de St Vincent (not seen); Heldreich s.n. (E; K; LE - syntypes).
Morina tournefortii Jaub. \& Spach, Illustr. 5: t. 429 (1854). Type: Armenia circa urbem Erzeroum, Tournefort s.n.; Asie minore, Aucher-Eloy s.n.; Jaubert s.n.; and Pinard s.n. (syntypes, not seen).
Morina subinermis Boiss., Diagn. II, 6: 94 (1859). Type: Turkey, in Bithynia. Duparquet (not seen).
Morina persica subsp. turcica Hal. in Oester. Bot. Zeit. 41: 409 (1891). Type: Macedonia prope Demirkapu, 19.8.1889, Farmanek s.n. and Tekir Dagh, in saxis promontorii Hodja Burnu, inter pago Panidos et Kumbaos litoris Propontidis, 2.7.1890, Degen s.n. (not seen).
Morina turcica Degen \& Hal. ex Čelak. in Bot. Jb. 17: 396 (1893), nom. nud. (Art. 32.1).
Morina spectabilis Gontsch. nom. nud. (Art. 32.1) ?in Herb. LE, cited by Komorov in Fl. U.R.S.S. 24: 8 (1957).

Robust herbs often forming large clumps of sterile rosettes and flowering shoots. Rhizome woody, the top often covered with the fibrous remains of old leaves. Leaves of sterile shoots and lower stem leaves up to $25 \times 2 \mathrm{~cm}$, 3-4 per whorl, glabrous, $\pm$ linear, with fairly regular 2-5 lobed, narrowly triangular teeth, petioles broad based, connate, forming short sheaths of 2-3 mm . Upper stem leaves smaller, similar to the lower leaves, but petioles scarcely connate or free, 3-4 leaves per whorl. Flowering stems erect, up to 1.25 m . Stems densely villous and glandular, square stemmed above, becoming terete or somewhat ridged and with fewer hairs below. Flowers sessile or shortly-stalked, up to 50 or even more per whorl, in up to 8 (rarely more) whorls, sometimes with small flowering shoots in the axils of the upper leaves. Whorls usually well separated from one another, the uppermost sometimes confluent. Bracts very variable, usually twice as long as the calyx whorls, linear with long acuminate tips, gradually tapering into a long spine, or broadly ovate with a shortly spiny acute apex; almost glabrous to densely villous and glandular, spiny, sinuate-dentate and similar to the leaves to almost entire with few spines. Bracts of lower whorls free or slightly overlapping at the base, upper bracts free or very rarely connate. Involucel cylindrical campanulate, tube $7-10 \times 3 \cdot 5-5 \mathrm{~mm}$, densely villous and with sessile glands and stalked glandular hairs to almost glabrous; teeth (8-) 10-14 $(-16)$ of varying lengths, two usually much longer than the others, the longest much exceeding the tube or rarely equalling it, often up to 14 mm or more at anthesis, the 2 longest teeth broad based, laminate at anthesis, becoming inrolled and rigid at maturity. Calyx $\pm$ glabrous, or very shortly pubescent outside, with a tuft of long white hairs at the base, tube broad, often as wide as deep, 3-5 mm long, lips often much longer than the tube, apex obtuse, nearly truncate or very shallowly emarginate. Corolla white, becoming pink or red, the tube very long and narrow 35-45 mm , with or without simple and glandular hairs, the throat somewhat swollen; limb $\pm 2$-lipped, the upper 2-lobed, the lower 3-lobed, lobes $12 \times 6 \mathrm{~mm}$ or more. Fertile stamens 2, filaments 9 mm or more, inserted at the top of the tube; anther lobes subequal. Staminodes minute, heart shaped, inserted $4-5 \mathrm{~mm}$ below the mouth of the corolla, below the anterior lip. Nectary 1, 3-lobed, anterior at the base of the corolla tube, Style longer than the stamens, stigma disc-shaped. Achenes rugose, adaxial face, $\pm$ convex, somewhat longitudinally furrowed, abaxial face furrowed, transversely rugose, apex obliquely truncate.

Observations: The protologue in the original Linnæan description refers directly with an unmodified descriptive phrase to Hortus Cliffortianus. For this reason, a specimen in that collection would be a preferred choice for typification. However, since there is no Morina specimen in that herbarium, the fragmentary material in the Linnæan herbarium (corolla only) has been adopted as the best available alternative. The geography of the group and morphology of the corolla leave little doubt as to the validity of the typification.

Plants from the Mussoorie area of India were described by Royle as M. wallichiana, nearly allied to M. persica, but having spiny lobed leaves, the upper stem and corolla softly villous, and the calyx lobes entire or shortly emarginate. The type specimen is a plant with rather ovate bracts and few spines, and corresponds closely with a number of specimens seen by us from this area. These tend to be greyer in colour and with fewer spines on the margins of the bracts than typical M. persica. However, a range of bract variation occurs in M. persica from broadly ovate
to narrowly linear, with apices acute and shortly spined to narrowly acuminate and long spined, the plants from Mussoorie being at one end of the variation range and not meriting the retention of specific rank. Although many plants of this kind appear to occur in the Mussoorie area, similar individuals have also been seen throughout the remainder of the range of $M$. persica, from Afghanistan to Bulgaria. We do not, therefore, consider Royle's taxon to merit retention as a geographically based subspecies, and it is best considered as a rather extreme form within the overall variation pattern of M. persica. An interesting specimen collected in the Muree Hills of Pakistan (Prescott Decie s.n. 1915) is probably another extreme variant of M. persica, one specimen on the sheet having leaves that are almost entire or with very small teeth. The bracts are broadly lanceolate, entire or with a few simple teeth, the upper whorls are connate, forming a small funnel-shaped sheath. The corollas have a dark coloured blotch on the lower lip; the colour appears to be yellow, but there is no field note in support of this conjecture. The specific rank of M. subinermis is maintained by Matthews (1972). It is known only from the type, which we have not seen. It should probably be regarded as a synonym of $M$. persica, as the description is in accord with the variant described above (Prescott Decie s.n., 1915).

Distribution and ecology: M. persica is distributed across western Asia and reaches southeastern Europe in Bulgaria, Romania, and Greece. It is widespread in Turkey, Iran, Israel, and Lebanon. It is common in Afghanistan, Kashmir, and Pakistan, where its range overlaps those of $M$. longifolia and $M$. coulteriana. This species occurs at lower altitudes than any other members of the Morinaceae, being found at altitudes below 500 m in Turkey, although it has been recorded from 3730 m in Afghanistan. It is a species of dry rocky places, steppe, and semi-desert and is often found as a roadside weed. It appears to tolerate both acid and alkaline soils, and is noted as growing on sandstone, dry granite, limestone, chalk, etc. Flowering normally seems to occur from May to August, but it has been also reported in April, September, and October. According to the notes with Chick 144, the peasants of Iran are said to eat the seeds and describe them as being like rice.
4. Morina longifolia Wallich ex DC., Prod. 4: 644 (1830). Type: Gossain Than, Nepal, Wallich 426 (BM; K; E-type collection).
Morina elegans Fischer \& Avé-Lall. in Index Seminum Hort. bot. imp. Petropol. 8: 67 (1841). Type: In alpibus Himalaya, nota apud nos e seminibus a Cel. Candolleis acceptis (not seen).

Robust herbs forming clumps of sterile rosettes and flowering shoots. Rhizomes woody, the top often covered with the fibrous remains of previous year's leaves. Leaves of sterile shoots and lower stem leaves glabrous, linear to linear-lanceolate, up to $40 \times 4 \mathrm{~cm}$, with fairly regularly coarsely cut 4-5 lobed teeth, spiny tipped, the petioles fused to form deep sheaths of 25-45 mm. Upper stem leaves similar, usually 3 per whorl, smaller, sheaths 8 mm or less, or petioles barely connate. Flowering stems erect, up to 90 cm , somewhat square in transverse section and pubescent to villous above, glabrous and slightly ridged to terete below. Flowers in (4) 7-9 $(-11)$ whorls, some shortly pedicillate others sessile; the upper whorls confluent, becoming more separated as the inflorescence matures. Bracts broadly ovate to orbicular with an acute spiny tip, margins often with numerous short spiny teeth, villous below and on the margins, often with few hairs and glossy outer surface, the bases markedly overlapping. Involucel $\pm$ cylindrical, glandular-hairy, sometimes densely so, $7-10 \times 2 \cdot 5-4 \mathrm{~mm}$ with $(5-) 8-10(-13)$ teeth, 2 much exceeding the others, glabrous tipped and with adpressed hairs below, not or scarcely laminate, shorter than or rarely equalling the calyx tube at anthesis. Calyx $\pm$ glabrous or with short adpressed hairs on the lips, lobes shallowly bifid, apices of the lobules rounded or rarely slightly apiculate; tube $4.5-6 \times 2.5-4 \mathrm{~mm}$ at anthesis Corolla white, becoming pink then deep red, the tube with many glandular and a few simple hairs without, $20-30 \times 1-2 \mathrm{~mm}$, throat somewhat expanded, lobes of the lower limb somewhat spreading, upper lip $\pm$ patent, median lobe of lower lip $7 \times 3 \mathrm{~mm}$. Fertile stamens 2, filaments $1-2(-3) \mathrm{mm}$, with a tuft of hairs below the anthers, inserted just inside the throat of the corolla. Anther lobes unequal, the shorter sometimes $2 / 3$ or less the length of the longer. Staminodes minute, inserted $2-3.5 \mathrm{~mm}$ below the
mouth of the corolla, under the anterior lip. Nectary 1, 3-lobed, anterior at the base of the corolla tube. Style a little longer than the stamens, stigma disc-shaped or somewhat domed. Achenes with abaxial face rugose with diagonal veins, adaxial face with deep furrow and prominent longitudinal veins; apex somewhat obliquely truncate and crenulate.

Observations: The specimens of $M$. longifolia examined by us showed relatively little variation. Size differences occur, notably a specimen from Bhutan, Ludlow, Sherriff \& Hicks 1958, which is particularly robust, with leaves of up to $50 \times 8 \mathrm{~cm}$ and very large leafy bracts.

Distribution and ecology: M. longifolia is mainly distributed in the Himalayas and Hindu Kush, and is the only member of the genus to be found in Nepal and Bhutan. In the Punjab, western Kashmir, and Pakistan its range overlaps those of $M$. persica and M. coulteriana. It is a plant of high altitudes and we have seen no specimens from below 2000 m , the highest record, a specimen from Nepal, was reported from 4250 m , while most specimens are collected from between 3000 and 3750 m . It occurs in a wide range of wet and dry habitats, often on grassy slopes or under shrubs. The flowering period is from June to September, sometimes extending into October. This species is quite widely cultivated in Britain by discerning plantsmen, and in the authors' garden in Surrey it flowers in June and July, with occasional small basal shoots flowering in October. The flowering sequence has been described by Kerner (1881). He observes that the white flowers open at dusk, and are pollinated by night-flying moths, after which they turn red and bend away from the rest of the flowers in the whorl in the course of a few hours. This does not correspond to our observations as, in our plants, the flowers open in the daytime, becoming pink by the following day, and do not turn red until the third day. Examination of unopened flowers showed pollen already adhering to the stigmas, perhaps indicating that cleistogamy may occur in this genus, paralleling the probable cleistogamy in Cryptothladia.

## Specimens examined

In the following enumeration all the specimens examined during the course of this study have been listed, primarily by genera and species, and secondarily by collectors and specimen numbers. The location of all specimens is shown using the standard international abbreviations for the institutions concerned; a list of these will be found under the acknowledgements. Since the number of taxa is not very large, it should be reasonably convenient for curators to use the list as a means of checking identifications of further duplicates of the listed gatherings.
I.1. Acanthocalyx nepalensis (D.Don) M. Cannon

Beer, Lancaster \& Morris 9419 BM. Bor \& Kirat Ram 20444 K. Bowes Lyon 2058 BM; 3264 BM; 15126 BM; Bowes Lyon s.n. BM. Cave 53 E. Chu 2785 E. Clarke 12913 K. Cooper 62 BM, E; 99 BM, E; 258 BM, E; 1585 BM; 1699 BM, E; 2170 BM; 2533 BM; 2935 BM. Dobremez 337 BM; 380 BM. Dungboo 55 E; 8539 LE. Einarsson, Skarby \& Wetterhall 606 BM; 892 BM. Gamble 9520 K. Gould 904 K. Grikley s.n. LE. Grierson \& Long 2592 E; 2669 E. Hanbury-Tracy 28 BM; Hara, Kanai, Mutara, Togashi \& Tuyama 2863 K. Hingston 181 K; 386 K. Hobson in 1897 K. Hooker in 1849 K. King's collector 647 K; in 1888 LE; in 1886 LE. Kingdon-Ward 11808 BM; 19582 BM; E; s.n. K. Lall Dhwoj 167 BM, E. Lepcha 15 E. Lobbichler s.n. BM. Ludlow \& Sherriff 170 BM; 422 BM; 1792 BM; 8780 BM; 8799 BM, E; 9756 BM, E; 11022 BM, E. Ludlow, Sherriff \& Elliott 15184 BM, E; 15677 BM. Ludlow, Sherriff \& Hicks 16379 BM, E; 19088 BM; 20293 BM. Ludlow, Sherriff \& Taylor 4700 BM, E; 5518 BM, E. McCosh 322 BM. McLaren's collectors AC140 E. Maire 49 E. Morton 232 K. Polunin 329 BM; 627 BM; 1151 BM. Polunin, Sykes \& Williáms 78 BM; 1546 BM; 2329 BM; 4536 BM. Pratt 45 BM. Ramesh Bedi 366 K; 1066 K; s.n. K. Ribu \& Rhomon 5270 K. Richardson 245 BM. Rohmoo Lepcha 787 E. Schilling 394 K; 995 K. Sharma E 416 BM. Shreltow 5140 BM. Shrestha \& Joshi 220 BM. Smith 120 BM. Spencer-Chapman 418 K; 652K. Stainton 875 BM, E; 557 BM, E. Stainton, Sykes \& Williams 3192 BM; 3237 BM; 4652 BM. Waddell 18 BM. Wager 285 K. Williams 792 BM. Wallich 424 K. Younghusband s.n. K. Yu 19845 E; 19730 E. Zimmerman 694 BM.
1.2. Acanthocalyx delavayi (Franchet) M. Cannon

Delavay 52 (298) P; 90 P; in 1885 P; in 1887 K. Forrest 393 E; 4653 E; 5638 BM, E, K; 5670 BM, E, K; 6104 BM, E, K. Handel-Mazzetti 2989 E; 9754 E. Kingdon-Ward 9632 BM. McLaren's collectors L2A

BM, E, K; N66 BM, E, K. Manberg s.n. K. Monbeig 62 E, K; 140 E; s.n. K. Potanin s.n. K. Rock 3422 E; 3781 E; 16260 E, K; 18098 E; 23835 BM, E, K; 23942 E; 24610 BM, E, K; 24692 BM, E, K; 24980 BM, E, K. Schneider 1494 E, K. Sino-British Expedition 737 K. Soulie 71 pars K; 975 K. Tu 4493 PE. Wilson 3781 pars BM, K. Yü 22152 E; 22750 E.
I.3. Acanthocalyx alba (Hand.-Mazz.) M. Cannon

Cunningham 471 E. Delavay 91 K, P; in 1886 P, K. Dungboo 6434 K; s.n. K. Fang 4008 E, K, PE; 6036 E, K, PE. Farrer \& Purdom 215 E. Forrest 5832 BM, E, K; 2685 BM, E, K; 28444 BM, E; 28826 BM, E. Gould 2133 K. Hanbury-Tracy 51 BM. King's collector 547 K. Kingdon-Ward 5894 E, K; 7065 K. Ludlow \& Sherriff 8833 BM, E. Ludlow, Sherriff \& Elliott 14077 BM, E; 15370 BM, E. Ludlow, Sherriff \& Taylor 5017 BM; 6180 BM, E. McLaren's collectors AC163 E; L50A BM, E, K; N104 BM, E. Maire 2 BM. Potanin in 1885 K; in 1893 K. Pratt 202 BM; 232 pars BM, E, K; 696 K. Purdom 872 K. Rock $4636 \mathrm{E} ; 5564$ BM; $12617 \mathrm{E}, \mathrm{K} ; 13119 \mathrm{BM} ; 14611 \mathrm{E} ; 16404 \mathrm{E} ; 17406 \mathrm{E}, \mathrm{K} ; 24113 \mathrm{BM}, \mathrm{E}, \mathrm{K} ; 24885$ pars BM, E, K. Schneider 3426 K; 3639 K; 3680 K. Soulie 71 pars K; 577 K. Wilson 3781 pars BM, K. Yu 8671 BM; 13625 BM, E; 15252 BM, E.
Intermediates between $A$. nepalensis and $A$. delavayi
Chu 2785 BM. Forrest 7155 E; 14022 E; 27124 E. Gould 511 K. Kingdon-Ward 325 K. Lowndes L1125 K. Ludlow, Sherriff \& Elliott 13894 BM. Ludlow, Sherriff \& Hicks 16573 BM; 19017 BM. McLaren's collectors 309D BM, E, K; B73 E, K. Maire 49 E; 66 E; 69 E; 82 E; 86 E; 128 BM, E; 715 E; 729 E. Potanin s.n. K. Pratt 45 BM, K. Rock 17725 BM, E; 17823 E; 24072 BM, E, K.

Intermediate between $A$. nepalensis \& A. alba
Gregory B 99 K. King's collector 8 K. Pratt 232 BM, E, K.
II.1. Cryptothladia chinensis (Pai) M. Cannon

Ching 539 E. Fang 4270 E, K, PE. Hao 1002 PE. Licent 4548 BM, K. Potanin in 1885 K; s.n. K. Przewalsky s.n. K. Rock 12556 BM, LE; 12952 E, K. ? collector 1792 PE; 6129 PE.
II.2. Cryptothladia parviflora (Karelin \& Kir.) M. Cannon

Gubanov 915 MW. Gukun s.n. BM. Karelin \& Kirilov s.n. BM, K. Konsevyanova s.n. MW; Regel 21798 BM, E, K, LE; s.n. K, LE. ?collector 4484 PE.
II.3. Cryptothladia kokonorica (Hao) M. Cannon

Gould 2217 K. Ludlow \& Sherriff 8691 BM. Morton 134 K. Richardson 124 BM. Spencer-Chapman 129 K; 649 K. Thorold 138 K. Wollaston 146 K. Younghusband 105 K. ?collector 6114 PE.
II.4. Cryptothladia chlorantha (Diels) M. Cannon

Ching 539 E. Forrest 2482 E, K; 5777 BM, E, K; 10212 E, K; 21255 E, K; 28801 BM, E. McLaren's collectors N9 BM, E, K. Rock 5129 E; 16499 E; 23834 BM, E, K. Sino-British Expedition 1641 K. Wilson 3781A BM, K. Yü 15306 BM, E. ?collector 5482 PE.
II.5. Cryptothladia polyphylla (Wallich ex DC.) M. Cannon

Bowes Lyon 2210 BM. Cummins s.n. K. Dobremez 501 BM. Dungboo s.n. K. Einarsson, Skarby \& Wetterhall 209 BM; 1193 BM. Gardner 1419 BM. Grey Wilson \& Phillips 741 K. King's collector 402 K. Lall Dhwoj 0402 BM. Ludlow, Sherriff \& Hicks 16243 BM, E; 17459 BM. Malla 9176 BM. McCosh 381 BM. Polunin 668 BM; 1339 BM. Polunin, Sykes \& Williams 4177 BM. Schilling 436 K. Shrestha 5126 BM. Stainton 4325 BM. Stainton, Sykes \& Williams 1763 BM; 2984 BM; 6138 BM. Wallich 425 K, PE. Wigram 122 K .
II.6. Cryptothladia ludlowii M. Cannon

Cooper 4525 BM. Kingdon-Ward 12383 BM, K; 14310 BM. Ludlow, Sherriff \& Hicks 16903 BM, E; 19050 BM, E; 20305 BM.
III.1. Morina kokanica Regel

Galubev s.n. MW. Gnezdillo 186 BM. Gomolitzsky s.n. E, K. Von Knorring 765 K. Linczevski \& Roshkova 39 K. Minkvitz 41766 BM, E, K. Neustrueva \& Knorring 4176A BM, E, K. Neustrueva 157 BM. Pavlov 71 MW; 396 MW; 482 MW. Regel 6/1880 BM, K, LE; 7/1880 BM. Sovetkina 1050 BM. Tilchko s.n. BM. Vatolkina 447B E, K.
III.2. Morina coulteriana Royle

Aitchison 407 BM, K; 746 K, LE. Anders 10979 W. Battel s.n. K. Bellew s.n. K. Benham 1919 BM. Bor 12289 K. Bowes Lyon 202 BM; 1095 BM, E. Bunge s.n. P. Capus 574 P. Carter 993 K. Chiddell

88 BM. Clarke 28767 BM; 30871 K. Collett 46 K. Cooper 5298 E; 5536 E. Drummond 14204 K; 22526 K. Duthie 935 BM, LE; 5661 BM; 25645 LE. Eckburg 9577 E. Edelberg 1783 W. Edgeworth 259 K. Ellis 272 K; 1348 K; 1881 K. Evershed s.n. BM. Furse 8048 E, K. Gibbons 607 E, K. Giles 58 K. Gronbczewsky s.n. K. Gukun s.n. MW. Harbuckle s.n. K. Harriss 16234 BM. Hedge 449 K. Hedge \& Wendelbo 5228 E; 9444 E. Huggins 228 BM. Kaletkina 38 K. Kingdon-Ward 11996 BM. Koelz 13012 W. Komorov s.n. LE. Kurushkaya \& Nicrasov 0887 BM. Lace 219a E; 1652 E. Lindbery 668 W; 917 W. Ludlow \& Sherriff 1419 E; 1828 BM, E; 5719 BM, E; 8219 BM; 9123 BM. Ludlow, Sherriff \& Taylor 5481 BM. Munro 1324 K. Neubauer 662 W. Novitsky s.n. LE. Parmanand 598 E. Pinfold 323 BM. Podlech 12348 E. Rechinger 31615 W. Regel s.n. BM. Reid III216 E. Rich B1082 K; 1095 K. Robson 2103 BM. Royle s.n. K. Schlagintweit 4181 BM. Sherriff 7350 BM. Siddigh 2269 BM. Singh 1771 K. Stainton 2785 BM, E. Stewart 3754 K. Stewart \& Rahman 25376 BM. Strachey \& Winterbottom 3 BM, K. Thompson 210 K. Toppin 412 K. Vassiljeva 5487 BM, E, K. Watt 441 E. Wendelbo 59 BM, K. Zaprialiev \& Tekutvev 278 MW.
III.3. Morina persica L.

Aitchison 420 BM, K. Alava 10654 E. Amsel s.n. W. Anders 3738 W; 10722 W. Anderson 49 E. Archibald 2856 K. Ascherson 439 BM, E, K. Atchley 1034 K; 2239 K. Aucher-Eloy 754 BM, K. Balansa 796 BM, K. Balls 514 E, K; 1183 BM. Baytop 14357 E; 19927 E. Behboudi 1293E W. Bledencvii 5085 LE; 5723 LE. Bokhari \& Edmundson 2036 E. Börnmuller 786 K; 4518 K; 9496 BM, K; 11955 BM, E. Bourgeau 240 K. Borne 3694 K. Brant \& Strangways 549 K. Calvert \& Zohrab 388 BM, K. Carter 1309 K. Chick 144 K. Clarke 24494 BM; s.n. K; s.n. E. Constantintinon H1507 K. Coode \& Jones 2323 E. Cooper 4983 E. Crookshank 435 K. Darrah 467 E. Davis 10099 E, K; 16369 E, K; 20370 K; 46443 K; 47477 E, K. Davis \& Coode 36591 E. Davis, Dodds \& Cetik 19068 BM, E. Davis \& Hedge 30051A E, K; 31731 BM, E, K. Drummond 25808 E, K. Dudley 35872 E, K; 36089 E, K. Duthie 336 K; 15603 K; 21847 K. Edelberg 1108 W. Edmondson 580 E. Ehrenberg s.n. K. Ekim 36 E. Falconer 534 K. Flemburg 851 E. Flemming 20 E; 61 E; s.n. K. Fox s.n. K. Furse 4098 K. Gamble 4213A K; 4308A K; 22819 K; s.n. K. Gay s.n. K. Gerard s.n. BM. Gilli 3881 W; 3882 W. Grant 17684 W. Grebenchikoff in 1936 K; in 1938 K. Gubanov \& Pavlov 162 BM. Guichard T/42/60 K. Haghighi 6241T W. de Halacsy s.n. K. Haradjian 1248 E, K; 2360 E, K. Harsukh 15336 K. Haussknecht in 1865 BM, K; in 1885 K. de Heldreich 46 E, K, LE; 99 E; s.n. K. Hewer 998 K; 1352 E, K; 2042 K. Hisbourg s.n. K. Kashkauli s.n. W. Kerstan 1447 W. Khan, Prance \& Ratcliffe 276 E, K. Koelz 11744 E, W. Kotschy 549 BM, K, LE. Kotte s.n. K. Lace 3869 E, K. Lack 4288 E. Lambert \& Thorp 559 K. Lammond 2478 E. Leonis s.n. LE. Liston s.n. E, K. Loftus s.n. BM, K. Madden s.n. E. Manisadjan 56 K; 112 K; 145B K. Marten 16 E. Mill s.n. K. Mooney 4514 K. Moussari \& Transhahr s.n. W. Neubauer 202 W. Orphanides 101 E, K. Parkinson 7366 E. Parry 251 E. du Pavillon 15 BM, K. Pichler s.n. K. Post s.n. BM. Price 916 K. Rechinger 5761 W; 16966 W; 31056 K, W; 32262 W; 34355 W; 47483 K, W. Rich 179 K. Rix 86 E. St Lager s.n. K. Sawyer 53 E. Sibthorpe s.n. K. Siehe 232 BM; 318 E. Smith 4107 BM. Stainton \& Henderson 5452 K. Stanf 403 K. Stewart s.n. E, K. Stribrny 66 E; 68 E; s.n. E, LE. Tebey 2007 E; 2669 E. Thompson 49 BM, E; 654 BM. Thompson \& Clarke s.n. K. Transhahr \& Moussari s.n. W. Walne s.n. LE. Warr 10099 K. Watson 275 K. Watt 45 E; 90 E. Wendelbo 831 W. Wiedermann s.n. BM, K. Winter 308 BM. Woronov s.n. LE. Zorab 404 K .
III.4. Morina longifolia Wallich ex DC.

Abel 78 BM; Bailey's collectors s.n. BM. Aitchison 47 K; s.n. LE. Bhattacharya 24331 LE. Bis Ram 530 BM. Burtt 1215 E. Clarke 24238 K; 31086 BM. Cooper 4914 BM, E; 5106 E; 5597 E. Duthie 935 LE; 1157 LE; 13115 BM, E; s.n. BM, LE. Dobremez 521 BM. Einersson, Skarby \& Wetterhall s.n. BM. Falconer 533 K. Fuller 854 K. Gamble 1495A K; 5666A K; 6518C K; 26917 K. Giles 727 K. Griffiths 2132 BM. Komorov s.n. LE. Lace 367 BM, E; 1497 BM, E. Lall Dhwoj 103 BM, E; 0608 BM, E. Lance 134 K. Lawrie 5448 BM. Lowndes 1376 BM. Ludlow \& Sherriff 3567 BM; 7819 BM, E; 8275 BM; 9226 BM. Ludlow, Sherriff \& Hicks 19581 BM, E. Maclagan 711 BM. Nand 251 E. Osmaston 67 K. Parker 3043 LE. Polunin 56/256 BM, E; 1449 BM. Polunin, Sykes \& Williams 208 BM; 2608 BM; 4358 BM; 4423 BM. Ram 8942 E. Reid s.n. E. Rich 1255 K. Ribu \& Rhomon 5509 E. Schlagintweit 10016 E. Schlich s.n. E. Sherriff 7373 BM. Stainton 4961 BM. Stainton, Sykes \& Williams 1964 BM; 3388 BM; 3475 BM; 7376 BM. Stewart 44 E; 45 E. Strachey \& Winterbottom 1 BM, LE. Thompson s.n. E. Venning K141 K. Wallich 426 BM, K. Watt 91 BM; 109 E; 445 E; 1944 E; 3300 E; 8833 E; 9597 E. Wigram 76 E. Young s.n. BM.

## Acknowledgements

In addition to the material in the British Museum (Natural History) (BM), we have also made extensive use of the collections preserved in the herbarium of the Royal Botanic Gardens, Kew (K). We are most grateful to the directors and staff of the following institutions, who have made specimens available to us on loan: Royal Botanic Garden, Edinburgh (E), Komorov Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE), Biology Department of the Lomonsov State University of Moscow (MW), Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris (P), Institute of Botany, Academia Sinica, Beijing (PE), and Botanische Abteilung, Naturhistorisches Museum, Wien (W).

We are most grateful to our colleague Dr S. Blackmore for his co-operation with the palynological aspects of this investigation, and especially for his personal contribution of the palynological section of this paper. We are also very appreciative of the help afforded by Dr C. J. Humphries who, in the course of extensive and most useful discussions, brought his wide experience of modern techniques in phylogenetic systematics to bear on relationships in the Morinaceae, and so helped to clarify our own ideas. We are also grateful to Dr J. R. Edmonson of the Merseyside County Museums for information on the Royle Herbarium, to Miss K. P. Kavanagh for assistance with the Latin description, to Mr J. R. Press for advice on mapping and to Mrs S. M. Burton for typing the final manuscript. Lastly, we acknowledge the help of Mr A. O. Chater, Dr N. K. B. Robson and Mr J. D. A. Stainton, through much helpful discussion at various stages during the course of the work.

## References

Bentham, G. \& Hooker, J. D. 1873. Genera plantarum 2: 158. London.
Blackmore, S. \& Cannon, M. J. 1983. Palynology and systematics of the Morinaceae. Rev. Palaeobot. Palynol. 40: 207-226.
Bobrov, E. G. 1957. Family CLV. Morinaceae (Dum.) Van Tiegh. In V. L. Komarov, Flora of the U.S.S.R. 24: 3-9. (Trans. Lavoott, Jerusalem 1972).

Bunge, A. 1852. Beitrag zur Kentniss der Flor Russlands: 321-323. St Petersburg.
Candolle, A. P. de 1830. Prodromus systematis naturalis regni vegetabilis 4: 644. Paris.
Coulter, T. 1824. Mémoire sur les Dipsacaceés. Mém. Soc. Phys. Hist. nat. Genève 2: 13-60.
Crété, P. 1981. Embryo. In P. Maheshwari (Ed.) Recent advances in embryology of angiosperms: 171-220. Delhi.
Cronquist, A. J. 1981. An integrated system of classification of flowering plants: 1013-1016. New York.
Erdtman, G. 1945. Pollen morphology and plant taxonomy III. Svensk bot. Tidskr. 39: 186-191.

- 1960a. Notes on the finer structure of some pollen grains. Bot. Notiser 113: 285-288.
-1960b. The acetolysis method. A revised description. Svensk bot. Tidskr. 54: 561-564.
Hemsley, W. B. \& Pearson, H. H. W. 1902. The flora of Tibet or high Asia. J. Linn. Soc. (Bot.) 35: 254-257.
Heywood, V. H. (Ed.) 1978. Flowering plants of the world: 261-262. Oxford.
Hutchinson, J. 1973. Families of flowering plants, ed. 3: 584-585. Oxford.
Kachidze, N. 1929. Karyologische studien über Familie der Dipsacaceae. Planta 7: 484-502.
Kamelina, O. P. \& Yakovlev, M. C. 1974. Development of the embryo sac in the genus Morina. Bot. Zh. S.S.S.R. 59: 1609-1617. [In Russian.]

1976. The development of microsporogenesis in representatives of the Dipsacaceae and Morinaceae. Bot. Zh. S.S.S.R. 61: 932-945. [In Russian.]
Kerner von Marilaun, A. 1881. The natural history of plants 2: 222 \& 351-353. London. (Trans. Oliver 1894-95).
Kingdon-Ward, F. 1936. Sketch of the vegetation and geography of Tibet. Proc. Linn. Soc. Lond. 1936: 142.

Linnaeus, C. 1738. Hortus cliffortianus: 14. Amsterdam.
-1753. Species plantarum: 28 . Stockholm.
Matthews, V. A. 1972. Morina L. In P. H. Davis (Ed.) Flora of Turkey 4: 581-582. Edinburgh.
Meusel, H. 1971. Mediterranean elements in the flora and vegetation of the western Himalayas. In P. H. Davis, P. C. Harper, \& I. C. Hedge, Plant life of southwest Asia: 53-72. Edinburgh.
Pai, Y. Y. 1938. Die Chinesischen Arten der Gattung Morina. Reprium Spec. nov. Regni veg. 44: 114-124.
Poucques, M. L. de. 1949. Récherches caryologiques. Revue gén. Bot. 56: 114-115.
Rafinesque, C. S. 1820. Tableau analytique des Ordes Naturels . . . Annls gén. Sci. phys. Brux. 6: 88.
Risse, K. 1929. Beiträge zur Zytologie de Dipsacaceen. Bot. Arch. Berlin 23: 266-288.
Spach, E. 1841. Histoire naturelle des vegetaux: phanerogams 10: 313. Paris.

Stainton, J. D. A. 1972. Forests of Nepal: 138-169. London.
Takhtajan, A. L. 1954. Origins of angiospermous plants: 62. Washington. (Trans. Gankin \& Stebbins, 1958).
-1980. Outline of classification of flowering plants. Bot. Rev. 46: 225-359.
Thorne, R. 1976. Phylogenetic classification of Angiospermae. Evolut. Biol. 9: 64.
Tieghem, P. E. L. van. 1909. Remarques sur les Dipacacées. Annls Sci. nat. (Bot.) IX, 10: 148-200.
Tournefort, J. P. de. 1703. Institutiones rei herbariae: 48. Paris.
Vaillant, S. 1724. Classe des Dipsacées. Hist. Acad. Sci. Paris 1722: 184-243.
Verlaque, R. 1976. Contributions à l'étude cytotaxonomiqe des Dipacacées \& Morinaceae du bassin Mediterranean. Thesis - University de Provence.
-1977. Rapports entres les Valerianaceae, les Morinaceae \& les Dipsacaceae. Bull. Soc. bot. Fr. 124: 475-482.
Vijayaraghavan, M. R. \& Sarveshwari, G. S. 1968. Embryology and systematic position of Morina longifolia. Bot. Notiser 121: 383-402.
Vinokurova, L. V. 1959. Palynological data to the systematic position of Dipsacaceae and Morinaceae. Problemy Bot. 4: 51-67. [In Russian.]
Wagenitz, G. 1964. In H. Melchior \& E. Werdermann (Eds.) Engler's Syllabus der Pflanzenfamilien 12th ed. 2: 477.

## Taxonomic index

Accepted names are in roman and synonyms in italic; new names are in bold, as are principal references. An asterisk ( ${ }^{*}$ ) denotes a figure or map.

Asaphes Spreng. 24
Barleria crotalaria A. Léveillé 12,14
Acanthocalyx (DC.) M.Cannon 2, 3, 5, 6*, 7, 8*, 9, $10^{*}, 11,13$
alba (Hand.-Mazz.) M.Cannon 9, 10*, 11, 14-15, 32
delavayi (Franchet) M.Cannon 9, 10*, 11 , 12-14, 15, 31
nepalensis (D.Don) M.Cannon 9, 10*, 11, 12, 13*, 14, 15, 31
Cryptothladia (Bunge) M.Cannon 2, 5, 6*, 7, 8*, 9, 15-17*, 31
chinensis (Pai) M.Cannon $15,16^{*}, \mathbf{1 7 - 1 8}$, 20, 32
chlorantha (Diels) M.Cannon $15,16^{*}, 17$, 19-20, 32
kokonorica (Hao) M.Cannon 15, 16*, 17 , 18, 19, 32
Iudlowii M. Cannon 2, 16*, 17, 22-24*, 32
parviflora (Karelin \& Kir.) M. Cannon 15, 16*, 17, 18-19, 32
polyphylla (Wallich ex DC.) M.Cannon 15 , 16*, 17, 20-22*, 32
Diototheca Vaillant 2
Morina L. $1,2,3,4,5,6^{*}, 7,8^{*}, 9,24,25^{*}, 28$
Sect. Acanthocalyx DC. 2, 3,9
Sect. Cryptothladia Bunge 2, 15
Sect. Diotocalyx DC. 2, 24
alba Hand.-Mazz. 9,14
aucheri Jaub. \& Spach 29
betonicoides Benth. 11,12
breviflora Edgew. 26
bullyana Forrest \& Diels 12
chinensis Pai 17, 18
chlorantha Diels 19
chlorantha var. subintegra Pax \& K. Hoffm. ex Limpr. 19
coulteriana Royle $2,24,25^{*}, \mathbf{2 6 - 2 8 *}, 30,31$, 32
delavayi Franchet 9, 12
elegans Fischer \& Avé-Lall. 2,30
graeca Jaub. \& Spach 29
kokanica Regel $4,24,25^{*}, 26,32$
kokonorica Hao 18, 19
lehmanniana Bunge 2,26,28
leucoblephara Hand.-Mazz. 9,14,15
longifolia Wallich ex DC. $2,4,22,24,25^{*}$, 30-31, 33
nana Wallich ex DC. 2,12
nepalensis D.Don 9,12
orientalis Miller 28
parviflora Karelin \& Kir. 2
parviflora var. chinensis Batalin 17
persica L. $2,4,22,24,25^{*}, 28-\mathbf{3 0}, 31,33$
persica subsp. turcica Hal .29
polyphylla Wallich ex DC. 2, 20, 22, 24
spectabilis Gontsch. 29
subinermis Boiss. 29,30
tournefortii Jaub. \& Spach 29
turcica Degen \& Hal. ex Čelak 29
verticillata Moench 28
wallichiana Royle 28, 29
Morinaceae J. Agardh $1,2,3,8,9$
Morinidia Raf. 2, 8

